ABUNDANCE, RECRUITMENT, AND ENVIRONMENTAL FORCING OF KODIAK RED KING CRAB

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By

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Abstract

Commercial harvests of red king crab *Paralithodes camtschaticus* around Kodiak Island, Alaska increased rapidly in the 1960s to a peak of 42,800 mt in 1965. Stock abundance declined sharply in the late 1960s, moderated in the 1970s, and crashed in the early 1980s. The stock has not recovered despite a commercial fishery closure since 1983. To better understand the rise, collapse, and continued depleted status of the red king crab stock around Kodiak Island, I conducted a retrospective analysis with three primary objectives: (1) reconstruct spawning stock abundance and recruitment during 1960–2004; (2) explore stock-recruit relationships; and (3) examine ecological influences on crab recruitment.

A population dynamics model was used to estimate abundance, recruitment, and fishing and natural mortalities. Three male and four female "stages" were estimated using catch composition data from the fishery (1960–1982) and pot (1972–1986) and trawl (1986–2004) surveys. Male abundance was estimated for 1960–2004, but limited data constrained female estimates to 1972–2004. Strong crab recruitment facilitated increased fishery capitalization during the 1960s, but the high harvest rates were not sustainable, likely due to reproductive failure associated with sex ratios skewed toward females.

To examine spawner-recruitment (S-R) relationships for the Kodiak stock, I considered lags of 5–8 years between reproduction and recruitment and, due to limited female data, two currencies of male abundance as a proxy for spawners: (1) all males ≥ 125 mm carapace length (CL); and (2) legal males (≥ 145 mm CL). Model selection involved AIC_c, the Akaike Information Criterion corrected for small sample size. An autocorrelated Ricker model using all males and a 5-year lag, with the time series separated into three productivity periods corresponding to different ecological regimes, minimized AIC_c values. Depensation at low stock sizes was not detected.

Potential effects of selected biotic and abiotic factors on early life survival by Kodiak red king crab were examined by extending the S-R relationship. Results suggested a strong negative influence of Pacific cod *Gadus macrocephalus* on crab recruitment. Thus, increased cod abundance and a nearshore shift in cod distribution likely impeded crab stock rebuilding.

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General Introduction

Waters around Kodiak Island in the northern Gulf of Alaska once supported the world's largest fishery for red king crab *Paralithodes camtschaticus*. A U.S. domestic fishery developed slowly during the 1930s to 1950s, as operators of purse seine vessels sought to supplement their summer salmon harvests by exploring crab fishing in the Kodiak area during winter. The lack of live tanks and small vessel size (i.e., < 18 m overall length) limited the fishery to nearshore areas adjacent to seaports with processing facilities. Annual landings increased rapidly in the 1960s to a peak harvest of 42,800 mt, worth $12.2 million ($0.13/lb) in 1965. However, annual harvests dropped sharply over the next few years, and then ranged from 4,900 to 10,900 mt before another sharp decline in the early 1980s resulted in a fishery closure in 1983. A variety of management actions, such as time and area closures and changes in minimum size limits, failed to stop the stock decline. Moreover, closure of the commercial fishery since 1983 has not resulted in recovery of this severely depleted stock. The collapse of this stock, and failure to recover after more than 25 years of fishery closures, remains a mystery.

To improve understanding of the conditions surrounding the rise, collapse, and continued depressed status of the red king crab stock around Kodiak Island, I conducted a retrospective analysis along three primary objectives corresponding to each of three chapters: (1) reconstruct the king crab spawning stock abundance and recruitment over 1960 to 2004; (2) estimate a stock-recruit relationship (if any); and (3) examine the

influences of biotic and abiotic factors on crab recruitment. However, as a first step in this understanding, ArcGIS was used to conduct geostatistical analyses of the spatial distribution of red king fishery removals over 1969 to 1982, as well as ADF&G survey catch distributions of Pacific cod *Gadus macrocephalus*, and Pacific halibut *Hippoglossus stenolepis*, two potential crab predators. This geospatial analysis is reported in Appendix A. A brief review in Appendix B considers selected population indices from the perspective of current management strategy criteria.

For objective 1, stock reconstruction, I applied a stock-synthesis approach that combines a variety of relative abundance and catch data to estimate abundance, recruitment, and fishing and natural mortalities during 1960–2004. The population dynamics model includes three male and four female "stages" derived from Alaska Department of Fish and Game catch composition data from the fishery (1960–1982), a pot (i.e., trap) survey (1972–1986), and a trawl survey (1986–2004). Stage-based analyses are particularly useful when age determination is problematic, as is the case for crab, but a "recruit" stage can be identified. Male abundance was estimated for 1960 to 2004, but the available data limited analysis of females to the years 1972 to 2004.

For objective 2, examination of potential spawner-recruitment (S-R) relationships for the Kodiak red king crab stock was based on abundance estimates derived from objective 1. The shape of the S-R relationship is a reflection of the average productivity of a stock at different stock levels and, thus, relates directly to fishery management objectives and the

choice of harvest strategies in order to maintain a target level of stock production. Additionally, recruitment is considered to be the primary determinant of dynamics of Alaskan crab populations. Due to the limited female data, male crab abundance was used as a proxy for both spawners and recruits. I also compared currencies of either all male crab $\geq$ 125 mm carapace length (CL) or legal male crab, defined as $\geq$ 145 mm CL, considered lag times of 5 to 8 years between reproduction and recruitment, and explored multiple periods of stock productivity within the examined time series. Several families of S-R models, including depensatory and autocorrelated, were considered.

To examine the influences of biotic and abiotic factors on crab recruitment, objective 3, the preferred S-R model that was derived through objective 2 for the Kodiak red king crab stock was modified to incorporate biotic and abiotic factors hypothesized to be important to the survival of early life stages of Kodiak red king crab. The datasets on predation and ocean conditions were limited to those with a temporal overlap with crab recruitment data. The combined spawner-recruitment model with environmental information provides a broader assessment of conditions surrounding the rise and collapse of the Kodiak king crab stock, as well as potential impediments to rebuilding (e.g., low spawning stock vs. predation vs. oceanographic conditions) that should be considered in ongoing restoration efforts.

Chapter 1: Reconstruction of Historical Abundance and Recruitment of Red King Crab during 1960–2004 around Kodiak, Alaska[1]

1.1 Abstract

Gulf of Alaska waters around Kodiak Island once supported the world's largest fishery for red king crab, *Paralithodes camtschaticus*. Fishery harvests occurred at low levels beginning in the 1930s, but increased rapidly in the 1960s to a peak harvest of 42,800 mt in 1965. However, stock abundance declined dramatically in the late 1960s, and again in the early 1980s. The history of the fishery included a variety of management measures, such as time and area closures and changes to minimum size limits. Despite these efforts, the stock was ultimately recognized as depleted, and a commercial fishery closure since 1983 has not resulted in a stock recovery. We developed a quantitative retrospective analysis to understand the conditions surrounding the rise, collapse, and continued depleted status of the red king crab stock around Kodiak Island, Alaska. Our approach used a population dynamics model to estimate abundance, recruitment, and fishing and natural mortality over time. The model included three male and four female "stages" and incorporated catch composition data from the fishery (1960–1982), a pot survey (1972–

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[1] Bechtol, William R., and Gordon H. Kruse. In press. Reconstruction of historical abundance and recruitment of red king crab during 1960–2004 around Kodiak, Alaska. Fisheries Research, doi:10.1016/j.fishres.2008.09.003.

1986), and a trawl survey (1986–2004). Male abundance is estimated for 1960 to 2004, but the available data limit analysis of females to the years 1972 to 2004. During a critical time of fishery development in the late 1960s, a chance period of strong recruitment helped promote the capitalization of this fishery. Very high harvest rates in the late 1960s were not sustainable, likely due to reproductive failure associated with sex ratios skewed toward females following a recruit-driven fishing period in the 1970s. Environmental and ecological changes, associated with a climate regime shift, likely exacerbated these problems.

1.2 Introduction

Waters around Kodiak Island in the northern Gulf of Alaska (Fig. 1.1) once supported the world's largest fishery for red king crab, *Paralithodes camtschaticus*. A U.S. domestic fishery developed slowly during 1930s–1950s, as operators of purse seine vessels sought to supplement their summer salmon harvests by exploring crab fishing in the Kodiak area during winter (Gray et al., 1965; Spalinger, 1992). The lack of live tanks and small vessel size (i.e., <18 m overall length) limited the fishery to nearshore areas adjacent to seaports with processing facilities. Annual landings increased rapidly in the 1960s to a peak harvest of 42,800 mt in 1965, dropped sharply over the next few years, and then ranged from 4,900 to 10,900 mt before another sharp decline in the early 1980s resulted in a

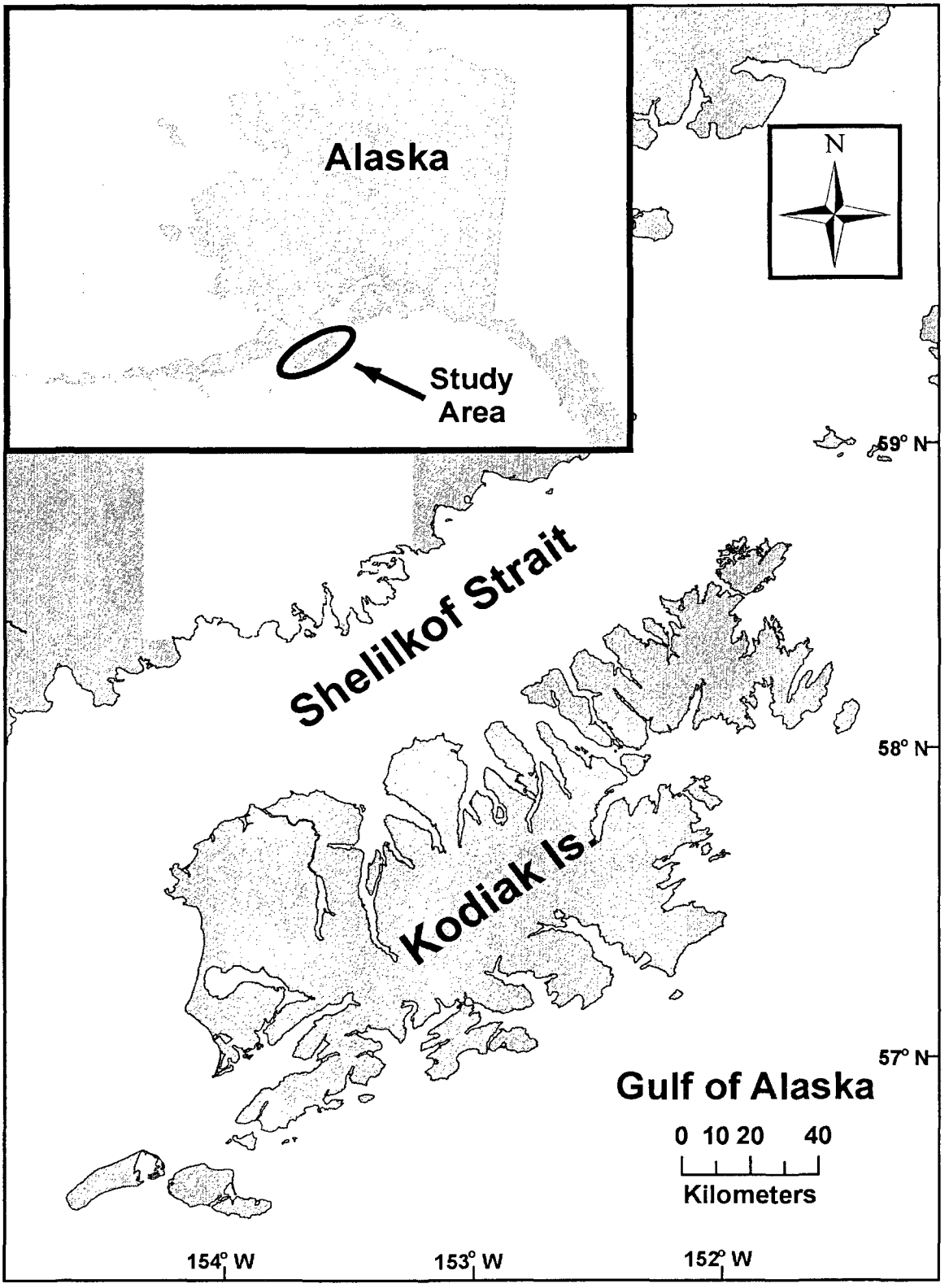

Figure 1.1. Study area around Kodiak Island, Alaska.

fishery closure in 1983 (Fig. 1.2; Spalinger and Jackson, 1994). A variety of management actions, such as time and area closures and changes in minimum size limits, failed to stop the decline of this male-only fishery (Gray et al., 1965; Spalinger, 1992). Moreover, closure of the commercial fishery since 1983 has not resulted in recovery of this severely depleted stock.

We conducted a retrospective analysis to better understand the conditions surrounding the rise, collapse, and continued depressed status of the red king crab stock around Kodiak Island. Our analysis estimates king crab spawning stock abundance and recruitment during 1960–2004 by using a stock-synthesis approach to combine a variety of relative abundance and catch data (Methot, 1990). Previously, Collie and Kruse (1998) developed a two-stage (i.e., recruit, post-recruit) catch-survey analysis model (CSA) for male red king crab in both Kodiak and Bristol Bay, and Collie et al. (2005) developed a three-stage (i.e., pre-recruit, recruit, post-recruit) CSA for male blue king crab, *Paralithodes platypus,* in the eastern Bering Sea. Stage-based analyses are particularly useful when age determination is problematic, but a "recruit" stage can be identified. The CSA uses survey and commercial catch data to generate estimates of survey catchability coefficients, measurement errors, and absolute abundance. We extended these efforts by developing a CSA that uses three stages of male crab and four stages of female crab to estimate abundances for the Kodiak red king crab stock during 1972–2004. In addition, a time series of abundance estimates based on a catch-length analysis (CLA) of male red king crab (Zheng et al., 1996) over 1964–1982 was extended back to 1960 using dockside

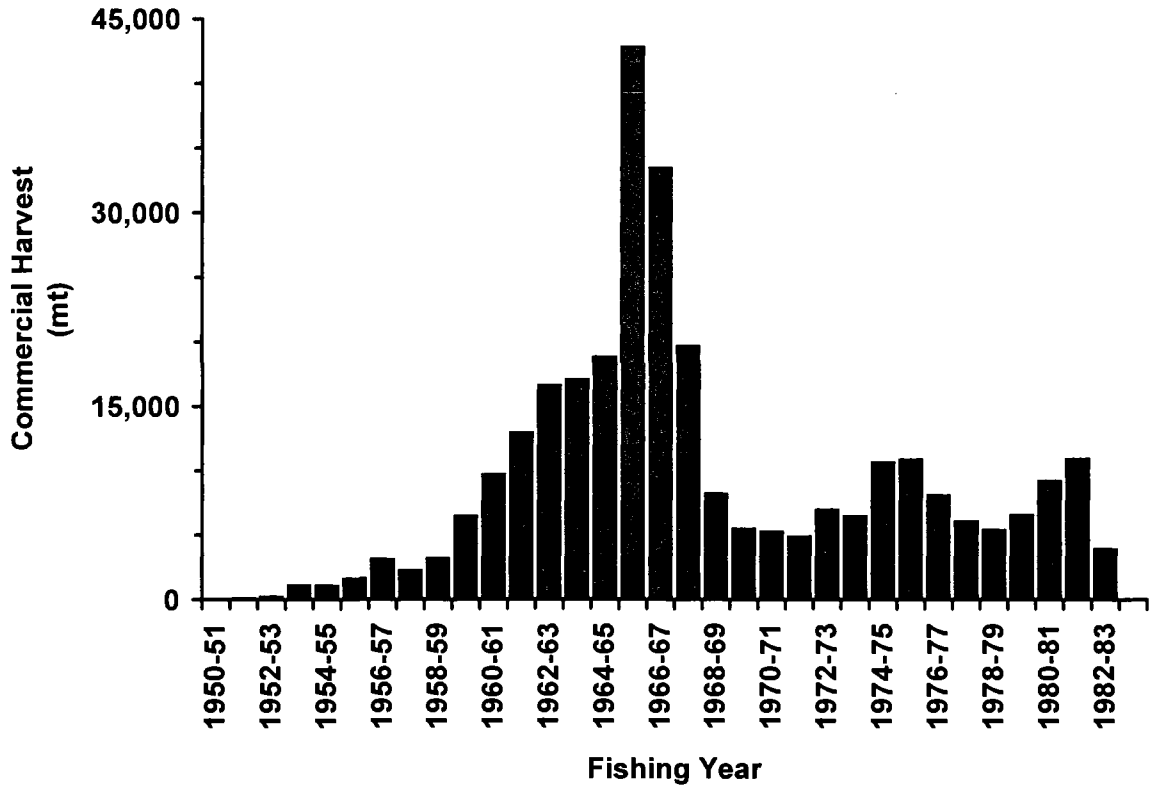

Figure 1.2. Annual harvests (mt) of red king cjrab from the Kodiak Management Area during 1950–1983.

sample data (Blau, 1988). The CLA is a length-based analogue to the age-based virtual population (cohort) analysis (Gulland, 1965). Our stock-synthesis reconstruction of the Kodiak red king crab stock merged these CSA and CLA analyses by incorporating commercial catch records from the Alaska Department of Fish and Game (ADF&G) fish tickets, dockside samples of landed crab, and relative abundance data from annual pot (i.e., trap) and trawl assessment surveys. Zheng et al. (1998) incorporated pot and trawl surveys, subsistence harvests, and summer and winter commercial fisheries data into a similar length-based synthesis model for red king crab in Norton Sound, Alaska.

Our population estimation models were developed in consideration of some general features of red king crab life history around Kodiak Island (Tyler and Kruse, 1995; NPFMC, 1998; Zaklan, 2002; Donaldson and Byersdorfer, 2005) The annual reproductive cycle is closely linked to the female molt. Adult females molt annually, regardless of size, from March through April. After molting, females extrude 40,000–500,000 ova which are fertilized by sperm transferred from a grasping male partner (Otto et al., 1990). The male molting period lasts several months starting in December, but males begin to "skip molt" (i.e., do not molt annually) with increasing frequency upon reaching approximately 125 mm carapace length (CL). Male crab can copulate with multiple females during the mating season, but laboratory studies found reduced fertilization success associated with smaller males and with secondary or later matings by a given male (Paul and Paul, 1990; Paul and Paul, 1997). In the wild, mating success with multiple females may be further constrained by factors such as the availability of mates,

synchrony of female molting, and the relatively short duration of the mating season. Embryos are incubated on the underside of the female's abdomen for approximately 300 d, and then hatch during March through May, after which the annual female reproductive cycle is repeated. The pelagic larvae inhabit the water column at depths <100 m until settling into a benthic existence between May and July in Kodiak; preferred habitat is nearshore (<50 m depth), rocky substrate with attached high-profile sessile fauna (Powell and Nickerson, 1965; Armstrong et al., 1993; Loher, 2001).

Juvenile crab molt through a series of instars in which the growth increment for both sexes is a linear function of pre-molt length up to approximately 60 mm CL (McCaughran and Powell, 1977). Molt frequency declines with increased carapace size, from 7 to 8 molts the first year after settlement to 1–2 molts in the fourth year. Greater molt frequency and larger size at age may occur in years of warmer water temperatures (Stevens, 1990; Stevens and Monk, 1990). Females grow more slowly than males, particularly after achieving 70 mm pre-molt CL (McCaughran and Powell, 1977). As red king crab age and grow, their distribution extends to progressively deeper depths (Armstrong et al., 1993; Stone et al., 1993). After achieving sexual maturity, adult crab migrate annually to shallower water for mating. In the Kodiak area, male size at physiological maturity (75–85 mm CL) is smaller than size at functional maturity (> 125 mm CL, i.e., size at which males have been observed in mating pairs). Mean age for male functional maturity is 7–8 years. Maximum red king crab age exceeds 20 years

(Matsuura and Takeshita, 1990), and maximum reported male size is 227 mm CL and 11 kg (Powell and Nickerson, 1965).

1.3 Methods

1.3.1 Data

1.3.1.1 Fishery Data

Fishery harvest data for 1960–1968 were primarily obtained from ADF&G published reports (e.g., Gray et al., 1965; Spalinger and Jackson, 1994; Cavin et al., 2005). Harvest data for 1969 through 1982 were obtained from the ADF&G TIX database (G. Smith and M. Plotnick, ADF&G, Juneau, pers. comm.). Although the Kodiak commercial fishery has been closed since 1983, limited king crab harvests have continued under subsistence fishing regulations. Commercial harvest data were pooled in accordance with State of Alaska guidelines to protect the confidentiality of individual landing records. Subsistence data are available for 1988 to present from ADF&G staff, but due to uncertainty about data quality, our analysis did not use these data.

In addition to collecting landings data, ADF&G conducted dockside sampling of male crab (n = 161,380) at primary landing facilities, including floating processors, around

Kodiak Island during 1960–1982 (Blau, 1988). Our analysis primarily used measurements of CL and shell condition. The shell condition of males was classified as newshell (molted within the past year), oldshell (did not molt within the past year), or very oldshell (has not molted for more than 1 year) using methods similar to Donaldson and Byersdorfer (2005) based on an inspection of the crab carapace, particularly with respect to erosion and presence of biofouling organisms. Because females molt each year and cannot be legally harvested, shell condition determinations are limited to males. For modeling purposes we assumed that carapace measurements were made without error.

1.3.1.2 Survey Data

Fishery-independent data were obtained from ADF&G. Pots (median effort of 1,895 annual pot pulls yielded data on approximately 17,800 male and 15,800 female crab annually) were used to conduct king crab assessment surveys around Kodiak Island during 1972–1986, notably after the large fishery decline in the late 1960s (Blau, 1985; Blackburn et al., 1990). Whereas fishery data provided information mainly on legal-sized males, surveys also generated information on females and sub-legal males. Survey data include vessel identifier, location, effort, and biological information on crab, such as size, sex, and shell condition, and also maturity status and clutch information for females (Donaldson and Byersdorfer 2005).

From 1980 to the present, ADF&G conducted an area-swept, multi-species bottom trawl survey around Kodiak Island. However, because the survey methodology and survey stations were less standardized with respect to crab assessment prior to 1986 (Dan Urban, Alaska Department of Fish and Game, Kodiak, pers. comm.), we only included trawl survey data after 1985. Although the primary target of the trawl survey was Tanner crab, *Chionoecetes bairdi*, this survey also provides an index of abundance for red king crab. Red king crab were caught in approximately 30 trawl tows annually, representing 10-15% of the survey effort. But, because the sample size was relatively low, (median annual catch of 68 male and 100 female crab since 1986), area-swept survey estimates of abundance have high variability and population composition estimates have low precision (Thompson, 1987).

1.3.2 Population Estimation Model

1.3.2.1 Overview

We developed a stock-synthesis model that incorporates a variety of methods and datasets to reconstruct Kodiak king crab abundance. The model reflects changes in data availability among years with pot surveys from 1972 to 1986, trawl surveys from 1986 to 2004, and commercial fishery data from 1960 to 1982. Fishery removals were allocated among the three crab stages based on dockside sampling data (Blau, 1988). The methodological foundations of our approach were a three- or four-stage CSA and a three-

stage CLA. During 1960–1971, prior to the start of fishery-independent surveys, only CLA could be conducted, and only for male crab; our CLA follows the approach of Zheng et al. (1996). The CSA used three male and four female stages to estimate crab abundances from 1972 to 2004 with different catchability and selectivity parameters associated with each survey platform.

1.3.2.2 Determination of Crab Stages

We defined the three stages of the male model as pre-legal, legal-recruit, and post-recruit. The minimum size limit for legal retention of male red king crab for most years in the Kodiak Management Area was 178 mm carapace width, equivalent to ~145 mm CL (Blau, 1988). The growth increment of adult males at this size is approximately 20 mm CL (McCaughran and Powell, 1977). Therefore, we defined legal-recruits as newshell males ≥145 mm CL and <165 mm CL, i.e., determined to have molted to a legal size within the previous year. Post-recruit males are defined as having been a legal size for at least 1 year and include oldshell and very oldshell males that are ≥145 mm CL and <165 mm CL, plus all males ≥165 mm CL regardless of shell condition. Pre-legal crab are believed to be one molt smaller than legal size and are defined as males of any shell condition that are ≥125 mm CL and <145 mm CL.

Estimation of the transitions among crab stages was based on the empirical growth model of; their model relied on data collected around the Kodiak area during the 1950s to 1970s

in tagging studies (n = 10,671 recoveries) and from observations of captive crab (Powell, 1967; Weber, 1967). The empirical model contains molting probabilities and molt increments (McCaughran and Powell, 1977) for male crab that are ≥125 mm CL and <165 mm CL.

Molt probability for male crab depends primarily on crab size and molt history. Molt history describes the progression of molting and skip-molting over a sequence of recent years. Given the data available from the different survey and fishery sampling platforms, conclusions on the molt history of sampled crab are limited to those crab that: (1) molted in the past year, defined as the year prior to the most recent survey or fishery; (2) not molted in the past year, but molted 2 years previously; and (3) not molted in the two previous years. Molt probability was estimated using the logistic model:

$$P = \frac{1}{1 + e^{-(25.0 - 0.17((L_0 - g)}} \quad , \tag{1.1}$$

where L_0 is pre-molt CL and g is a parameter (Table 1.1) based on molt history (McCaughran and Powell, 1977). Conditioned on the molt probability, the molt increment, $\hat{L}_i$, was estimated as a normal random variable in which the expected value depends on pre-molt length, L_0, and four additional parameters (a, b, c, and d; Table 1.1) that vary with molt history, whereas the variance of the increment, $\hat{\sigma}^2_{L_i}$, depends only on pre-molt size (McCaughran and Powell, 1977):

$$\begin{aligned} \hat{L}_i &= ae^{-\frac{(L_0-b)^c}{d}} \\ \hat{\sigma}^2_{L_i} &= 0.42L_0 - 0.104 \\ \hat{L}_{post} &= L_0 + \hat{L}_i \quad , \end{aligned} \tag{1.2}$$

where $\hat{L}_{post}$ is the estimated post-molt CL.

Post-molt frequency distributions were estimated with a Monte Carlo simulation using parameters from the McCaughran and Powell (1977) model (Table 1.1). Twenty replicates of 1,000 iterations were obtained for each 1 mm increment of pre-molt CL in the pre-legal and legal-recruit crab stages. Predicted post-molt distributions were then weighted by the size distribution of each shell condition observed in the pot survey from 1972 to 1986, and results pooled by crab stage.

Because female crab cannot be legally harvested, delineation of the female components of the population differed from the knife-edged definition of male crab stages based on the legal size limit. Four female stages were defined using a combination of size and maturity, which were both recorded during ADF&G pot and trawl surveys (Donaldson and Byersdorfer, 2005). To derive these stages, CL frequency distributions were compiled into mature and immature categories from the pot survey data, the most comprehensive data available for females. A maturity ogive by 1 mm CL interval was then calculated using a two-parameter logistic equation:

Table 1.1 Values of parameters *g*, *a*, *b*, *c*, and *d* used in Eqs. (1.1) and (1.2) for estimating molt probability for male crab and molt increment for male and female red king crab given their molt history.

		Molt probability		Molt increment			
Molt history[a]	Shell condition	Probability	*g*	*a*	*b*	*c*	*d*
a. Male crab							
MM	New	P(M|M,M,L_0)	2.5	19.45	117.5	2.0	11,000
MS	Old	P(M|M,S,L_0)	7.5	18.97	112.5	2.0	10,000
SS	Very Old	P(M|S,S,L_0)	25.0	18.05	102.5	2.0	8,000
b. Female crab							
MM	New	Molt annually		14.97	70.0	1.7	1,300

[a] M = molt, S = skip molt, L_0 = pre-molt carapace length; letters indicate whether the crab molted with the first letter signifying the past year, the second and third letters signify two and three years previously, respectively (McCaughran and Powell, 1977).

$$\theta = \frac{1}{1 + e^{-\beta(L-\alpha)}}, \tag{1.3}$$

where θ is proportion mature at carapace length L and α and β are parameters (Fig. 1.3). Estimated female size at 50% maturity of 101.5 mm CL agreed favorably with the 101.9 mm CL previously obtained for Kodiak red king crab (Pengilly et al., 2002). Using the growth model developed by McCaughran and Powell (1977) for Kodiak red king crab females, we back-calculated from the size of 50% female maturity to obtain a mean pre-molt size of 88 mm CL. We defined 88 mm CL as a lower bound for our female stages. Females 88–101 mm CL were defined as "small" crab and those >101 mm CL defined as "large" crab. Because virtually all immature crab are smaller than 130 mm CL (i.e., only 14 of 61,565 immature females reported in the pot survey database were larger than 130 mm CL), 130 mm was set as the upper bound of the immature stage. However, female crab exhibit substantial overlap between size and maturity status. Therefore, by combining data on maturity and size, the four female stages became: immature-small, mature-small, immature-large, and mature-large. Stage-specific parameters to describe growth and maturity transitions were estimated through 3,000 iterations of Monte Carlo simulations. Growth increments in immature-small females were estimated using Eq. (1.2) (McCaughran and Powell, 1977). Growth increments of immature-large females were estimated as a normal random variable with mean of 6.7% and standard deviation of 1.9% (Stevens and Swiney, 2006). Maturity transition rates were estimated from Eq. (1.3)

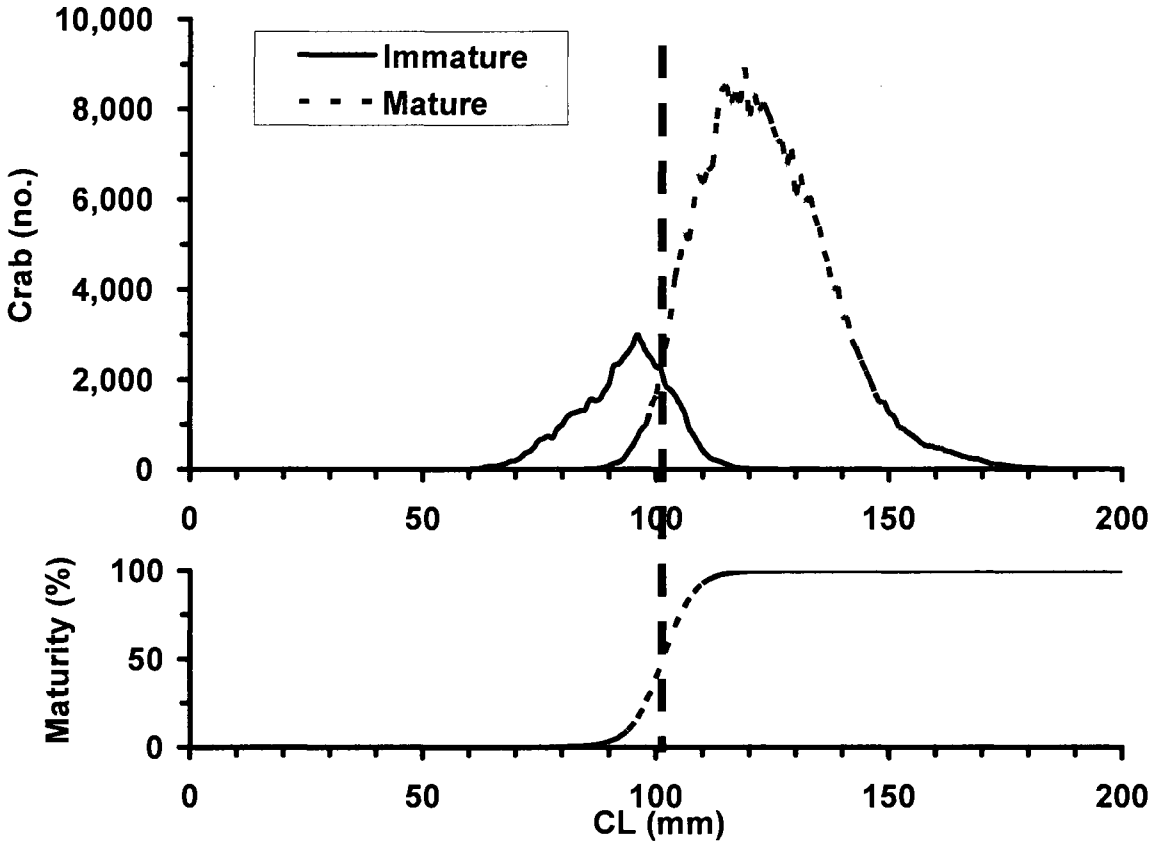

Figure 1.3. Size distribution of immature and mature female crab (upper panel) and corresponding mean female maturity schedule (lower panel) in the pot survey around Kodiak Island during 1972–1986. The vertical line shows the female size of 50% maturity.

applied to post-molt size distributions. To estimate maturity rates of post-molt immature-large females, post-molt growth distributions were calculated using Eq. (1.2), then maturity rates were applied from Eq. (1.2) (Stevens and Swiney [2006] had few samples of this stage). In all estimations, we assumed a uniform distribution on pre-molt size compositions.

In summary, the following crab stages are used in the model:

Male crab stages	
Pre-legal	125–144 mm CL
Legal recruit	145–164 mm CL newshell
Post-recruit	145–164 mm CL oldshell and all > 164 mm CL
Female crab stages	
Immature-small	88–101 mm CL immature
Mature-small	88–101 mm CL mature
Immature-large	102–130 mm CL immature
Mature-large	102–130 mm CL mature or >130 mm CL

1.3.2.3 Abundance Estimation

A general stock dynamics model was applied in which absolute abundance for a crab stage in year $t + 1$ is a function of abundance in year t, minus catch (including discard mortality in year t), plus or minus animals that molted into or out of the stage since year t, adjusted by natural mortality. Natural mortality is a particularly difficult parameter to

estimate due to confounding with recruitment, fishing mortality, and survey gear selectivity (Quinn and Deriso, 1999). For our analysis, female and male natural mortalities were set equal and two options for natural mortality schedules were considered. First, natural mortality was treated as constant among years and evaluated over a range of alternative values (0.1–0.9, in increments of 0.1) to facilitate comparisons with previous studies (Zheng et al., 1996; Collie and Kruse, 1998). While indicating the sensitivity of model parameter estimates to different inputs, crab abundance estimates generally increased, particularly prior to the 1986 start of the trawl survey, in response to larger values of fixed mortality.

Our second option treated natural mortality as a random walk, allowed to deviate between successive years but with a penalty, M_{pen}, assigned equal to the summed square of the deviations:

$$\begin{aligned} M_{t+1} &= M_t + \varepsilon_{M_t} \\ M_{pen} &= \sum_{t=1960}^{2003} \varepsilon_{M_t}^2 \quad , \end{aligned} \tag{1.4}$$

where M_t is natural mortality and ε_{Mt} is the natural mortality deviation. In a length-based population model for red king crab in Bristol Bay, Alaska, Zheng et al. (1995) found improved model fit when using four levels of time-dependent natural mortality compared to a constant mortality over time. Our second approach attempts to capture the more realistic expectation that natural mortality varies annually with ecosystem changes (e.g.,

water temperature or predator abundance), but that extreme deviations between sequential years occur infrequently (e.g., Hare and Mantua, 2000). In applying the random walk to the entire time series, a total of 43 deviations were calculated based on 45 years of data with no deviation for year 1 and no M for year 45.

For model estimation, the accounting year starts at the time of the survey with estimated abundance of $N_{a,t}$ for crab in stage a in year t. The fishery occurs at time lag τ_t, which is the fraction of a year between the survey and the mid-point of the fishery in year t. Pre-fishing crab abundance is then calculated as the starting abundance, adjusted for natural mortality, as in

$$N_{a,t+\tau_t} = N_{a,t} e^{-M_t \tau_t} \quad . \tag{1.5}$$

The parameter $\phi_{a,t}$, the rate at which crab in stage a are encountered by the fishery in year t, is a function of the instantaneous fishing mortality rate, $F_{a,t}$, which is essentially the total annual fishing rate, F_t for the population, adjusted by fishery selectivity for stage a crab:

$$\phi_{a,t} = 1 - e^{-F_{a,t}} = 1 - e^{-F_t s_{a,F}} \quad . \tag{1.6}$$

Fishery selectivity is a model-estimated parameter expected to be highest for post-recruit male crab because the fishery presumably targeted large males in order to minimize time spent sorting and discarding crab that could not be legally retained. Thus, $\hat{T}_{a,t}$, the total catch of stage a crab encountered by the fishery, becomes the product of crab abundance at time $t + \tau_t$ and the encounter rate, $\phi_{a,t}$, with an ultimate disposition as either retained catch, $\hat{C}_{a,t}$, or discarded catch:

$$\hat{T}_{a,t} = N_{a,t+\tau_t}\phi_{a,t} = \hat{C}_{a,t} + \left(\hat{T}_{a,t} - \hat{C}_{a,t}\right), \tag{1.7}$$

where discarded catch (i.e., at-sea discards) is defined as total catch minus the retained catch. It is assumed that all legal-sized crab captured by the fishery were retained, with no discards of legal crab due to aspects such as market considerations (e.g., for shell condition). Letting $\gamma_{a,t}$ be the portion of the total catch of crab stage a that may be legally retained in year t, estimated fishery retention becomes

$$\hat{C}_{a,t} = \gamma_{a,t}\hat{T}_{a,t} = \gamma_{a,t}N_{a,t+\tau_t}\phi_{a,t} \ . \tag{1.8}$$

For all female stages $\gamma_{a,t} = 0.0$, and for all legal-recruit and post-recruit males, $\gamma_{a,t} = 1.0$. However, due to individual growth variability, a portion of the crab defined as "pre-legal" males based on carapace length may actually be legally retained in terms of carapace width, such that $0.0 < \gamma_{\mathrm{PL},t} < 1.0$. Based on pot survey data, $\gamma_{\mathrm{PL},t}$ was set equal to 0.05. Because not all discards survive, a fixed handling mortality rate H was applied to

the discards such that population losses to discard mortality are represented by $\left(\hat{T}_{a,t} - \hat{C}_{a,t}\right)H$. Estimated total fishery-related losses at the time of the fishery become the sum of retained catch and discard mortality, i.e., $\hat{C}_{a,t} + \left(\hat{T}_{a,t} - \hat{C}_{a,t}\right)H$. For our analysis, we fixed H at 0.5 because model runs with fixed handling mortality values ranging from 0.1 to 1.0 indicated that results were relatively insensitive to the variation in H compared to the effects of other model inputs. Deducting fishery losses from stage a abundance at the time of the fishery, and adjusting for discard mortality during the fishery and natural mortality following the fishery, gives the surviving abundance of stage a crab at the start of accounting year $t + 1$:

$$S_{a,t+1} = \left[N_{a,t+\tau_t} - \hat{C}_{a,t} - \left(\hat{T}_{a,t} - \hat{C}_{a,t}\right)H\right]e^{-M_t(1-\tau_t)} . \tag{1.9}$$

Substituting from above and reorganizing gives:

$$S_{a,t+1} = N_{a,t}e^{-M_t}\left\{1 - \left(1 - e^{-F_t s_{a,F}}\right)\left[\gamma_{a,t} + \left(1 - \gamma_{a,t}\right)H\right]\right\} . \tag{1.10}$$

In years without a fishery, $F_t = 0$, so Eq. (1.10) becomes:

$$S_{a,t+1} = N_{a,t}e^{-M_t} . \tag{1.11}$$

Although Eq. (1.10) applies generically to both males and females, different equations result after adjusting for molting, as follows. After the year t fishery and prior to the start of accounting year $t + 1$, some stage a survivors molt. For modeling purposes, it is assumed that natural mortality does not differ before and after the molt. Using a growth transition parameter to represent the male crab molt, the recursive equations to estimate male crab abundances across stages and years, here represented by replacing "N" with "*Male*," become:

$$\begin{aligned}
Male_{PL,t+1} &= Male_{PL,t}e^{-M_t}\left\{1-\left(1-e^{-F_t s_{PL,F}}\right)\left[\gamma_{PL,t}+\left(1-\gamma_{PL,t}\right)H\right]\right\}G_{PL,PL}+I_{m,t+1}\\
Male_{LR,t+1} &= Male_{PL,t}e^{-M_t}\left\{1-\left(1-e^{-F_t s_{PL,F}}\right)\left[\gamma_{PL,t}+\left(1-\gamma_{PL,t}\right)H\right]\right\}G_{PL,LR}\\
&\quad + Male_{LR,t}e^{-M_t}\left[1-\left(1-e^{-F_t s_{LR,F}}\right)\right]G_{LR,LR}\\
Male_{PR,t+1} &= Male_{PL,t}e^{-M_t}\left\{1-\left(1-e^{-F_t s_{PL,F}}\right)\left[\gamma_{PL,t}+\left(1-\gamma_{PL,t}\right)H\right]\right\}G_{PL,PR}\\
&\quad + e^{-M_t}\left\{Male_{LR,t}\left[1-\left(1-e^{-F_t s_{LR,F}}\right)\right]G_{LR,PR}+Male_{PR,t}\left[1-\left(1-e^{-F_t s_{PR,F}}\right)\right]\right\}
\end{aligned} \tag{1.12}$$

in which $Male_{PL,t}$ is pre-legal, $Male_{LR,t}$ is legal-recruit, $Male_{PR,t}$ is post-recruit, and $I_{m,t+1}$ is new pre-legal male crab introduced into the model, and $G_{a,b}$ is the growth transition for the proportion of crab surviving and growing (molting) from stage a to b between years t and $t + 1$. Crab that fail to molt into another stage are represented as $G_{a,a}$.

Generic recursive equations for female crab are derived from Eq. (1.10) above by setting $\gamma_{a,t} = 0$ for all female stages (i.e., females may not be legally retained; Pengilly and

Schmidt, 1995). Estimated abundance of female stage a surviving from the start of year t to the start of year $t + 1$ is:

$$S_{a,t+1} = N_{a,t} e^{-M_t} \left[1 - \left(1 - e^{-F_t s_{a,F}}\right) H \right]. \tag{1.13}$$

By incorporating parameters to allow growth and maturity among stages, the recursive equations to estimate female crab abundances, here represented by replacing "N" in Eq. (1.10) with "*Fem*," are

$$\begin{aligned}
Fem_{IS,t+1} &= Fem_{IS,t} e^{-M_t} \left[1 - \left(1 - e^{-F_t s_{IS,F}}\right) H\right] \left(1 - G_{IS_g}\right)\left(1 - G_{IS_m}\right) + I_{f,t+1} \\
Fem_{MS,t+1} &= e^{-M_t} \left\{ Fem_{IS,t} \left[1 - \left(1 - e^{-F_t s_{IS,F}}\right) H\right] \left(1 - G_{IS_g}\right) G_{IS_m} + Fem_{MS,t} \left[1 - \left(1 - e^{-F_t s_{MS,F}}\right) H\right] \left(1 - G_{MS_g}\right) \right\} \\
Fem_{IL,t+1} &= e^{-M_t} \left\{ Fem_{IS,t} \left[1 - \left(1 - e^{-F_t s_{IS,F}}\right) H\right] G_{IS_g} \left(1 - G_{IS_m}\right) + Fem_{IL,t} \left[1 - \left(1 - e^{-F_t s_{IL,F}}\right) H\right] \left(1 - G_{IL_m}\right) \right\} \\
Fem_{ML,t+1} &= e^{-M_t} \left\{ Fem_{IS,t} \left[1 - \left(1 - e^{-F_t s_{IS,F}}\right) H\right] G_{IS_g} G_{IS_m} + Fem_{MS,t} \left[1 - \left(1 - e^{-F_t s_{MS,F}}\right) H\right] G_{MS_g} \right. \\
&\quad \left. + Fem_{IL,t} \left[1 - \left(1 - e^{-F_t s_{IL,F}}\right) H\right] G_{IL_m} + Fem_{ML,t} \left[1 - \left(1 - e^{-F_t s_{MLS,F}}\right) H\right] \right\},
\end{aligned} \tag{1.14}$$

with female stages of $Fem_{IS,t}$ as immature-small, $Fem_{MS,t}$ as mature-small, $Fem_{IL,t}$ as immature-large, and $Fem_{ML,t}$ as mature-large, and $I_{f,t+1}$ as a model-estimated parameter representing the introduction of new immature-small female crab into the model each year. Transitions from year t to $t + 1$ are: G_{IS_g} is the proportion of immature-small crab growing to large size; G_{IS_m} is the proportion of immature-small crab maturing; G_{MS_g} is the proportion of mature-small crab growing to large size; and G_{IL_m} is the proportion of immature-large crab maturing. Other parameters are similar to those for male crab.

To prevent drastic and unrealistic shifts in the annual fishing mortality rate between adjacent years, F_t was treated as a random walk process with a penalty proportional to the deviation between years:

$$F_{t+1} = F_t + \varepsilon_{F,t}$$
$$F_{pen} = \sum_{t=1960}^{1981} \varepsilon_{F,t}^2 \quad . \tag{1.15}$$

Predicted survey relative abundance indices were calculated for both male and female crab as the products of gear catchability and stage selectivity coefficients and absolute abundance estimates (Quinn and Deriso, 1999). Predicted pot survey catches of each crab stage were calculated as:

$$\hat{P}_{a,t} = N_{a,t} q_P s_{a,P} \quad , \tag{1.16}$$

where q_P is pot survey catchability, and $s_{a,P}$ is pot survey selectivity for stage a. Predicted trawl survey catches of each crab stage were similarly calculated as:

$$\hat{T}_{a,t} = N_{a,t} q_T s_{a,T} \quad , \tag{1.17}$$

where q_T is trawl survey catchability, and $s_{a,T}$ is trawl survey selectivity for stage a.

During model development, several constraints in estimated parameters were explored. For example, model performance was improved with catchabilities constrained to be ≤ 0.5, selectivities fixed at 1.0 for legal-recruit males in the surveys, and other selectivities constrained to be ≤ 1.0. Also, estimates of annual model recruitment were constrained to be positive. Based on the growth simulations of McCaughran and Powell (1977), female crab are assumed to recruit to our model between ages 4 and 5 and male crab between ages 6 and 7, on average, such that a given brood year recruits as females in year t and males in year $t + 2$. Until approximately age 4, male and female molt probabilities and growth increments are similar (McCaughran and Powell, 1977), and it is likely that male and female crab of a similar brood year have similar abundances and natural mortality until this age. To improve model performance by reducing the number of estimated parameters, the abundance of female recruits in year $t - 2$ was calculated as a function of year t male recruit abundance, lagged 2 years and adjusted for natural mortality as in,

$$I_{f,t} = I_{m,t+2} e^{(M_{t+1} + M_t)}, \tag{1.18}$$

where model recruit abundances are $I_{m,t+2}$ for males in year t+2 and $I_{f,t}$ for females in year t, and M_{t+1} and M_{t+2} are the estimated natural mortalities in the indicated year. Female recruitment for 2003 and 2004 was calculated as the median of recruitment in the preceding five years because male values for 2005 and 2006 were not estimated.

Model estimates of abundance were generated by comparing differences among observed and predicted catches in the fishery and both surveys. The residual sum of squares for retained catch (i.e., harvest), RSS_C, is calculated as the difference between the total observed and total predicted (from Eq. (1.8)) log-transformed harvest values by male crab stage for years 1960–1982:

$$RSS_C = \sum_{a=1}^{3} \sum_{t=1960}^{1982} \left[\ln\left(C_{a,t} + 0.001\right) - \ln\left(\hat{C}_{a,t} + 0.001\right) \right]^2 . \tag{1.19}$$

The addition of a small constant to both observed and predicted catches helps keep log-transformed values realistic. Log-transformed annual catch data can be assumed to have an additive error structure with lognormally distributed observation errors (Quinn and Deriso, 1999). The residual sum of squares for both the pot and trawl survey data were similarly calculated as the difference between the observed and predicted log-transformed values for each crab stage in a survey year:

$$RSS_P = \sum_{a=1}^{7} \sum_{t=1972}^{1986} \left[\ln\left(P_{a,t} + 0.001\right) - \ln\left(\hat{P}_{a,t} + 0.001\right) \right]^2 , \tag{1.20}$$

and

$$RSS_T = \sum_{a=1}^{7} \sum_{t=1986}^{2004} \left[\ln\left(T_{a,t} + 0.001\right) - \ln\left(\hat{T}_{a,t} + 0.001\right) \right]^2 , \tag{1.21}$$

where RSS_P is the sum of squared residuals for the pot survey index and RSS_T is the sum of squared residuals for the trawl survey index.

Estimates of model parameters for the Kodiak red king crab population were derived by minimizing the sum of squared differences between the observed and predicted values with the objective function:

$$RSS_{Tot} = \lambda_C RSS_C + \lambda_P RSS_P + \lambda_T RSS_T + \lambda_M M_{pen} + \lambda_F F_{pen} \,, \qquad (1.22)$$

where the λ's are the weights of the input datasets. Because the weighting scheme can have a large influence on which set of input data has the greatest effect on population parameter estimation, several weighting schemes were explored. To provide a standard for comparison, equal weighting with $\lambda_C = \lambda_P = \lambda_T = \lambda_M = \lambda_F = 1$ was used as a base case. Given the relative magnitude of differences between the mortality rate penalties and the squared residuals for other data, this standard placed higher emphasis on fishery catch and survey data for which direct observations were available for comparison. In addition, the greater number of fishery and survey catch data points contributing to the objective function further justifies equal weighting to emphasize catch data relative to weighting of mortality rate penalties. An alternative weighting was by the natural logarithm of the sample size (number of crab) in each dataset scaled relative to the smallest value, except that the logarithm of the number of calculated residuals is used for natural and fishing

mortalities lambdas ($\lambda_C = 3.88$, $\lambda_P = 4.31$, $\lambda_T = 2.81$, $\lambda_M = 1.22$, and $\lambda_F = 1.00$); this approach emphasizes the number of crab sampled for a particular dataset, particularly in the years of higher crab abundance. Finally, a sensitivity weighting was applied in which an individual dataset was given an arbitrary weight of 2, 5, or 10 while the remaining datasets were weighted at unity.

1.3.2.4 Model Implementation, Parameter Estimation, and Uncertainty

A minimum of 25 estimated parameters is used in common between male and female crab, including one catchability coefficient each for the pot survey and the trawl survey (i.e., catchability coefficients are set equal across sex but differ across data source) and 23 estimates of annual fishing mortality. In addition, the male component of the model uses 45 years of data and estimates 54 parameters including 3 starting abundances, 44 recruit abundances, and 7 selectivity parameters. The female component of the model uses 33 years of data and estimates 15 parameters including 3 starting abundances, and 12 selectivity parameters. Thus, a minimum of 94 total parameters was estimated in the model with up to 44 additional parameters estimated for the random walk option of natural mortality. A total of 171 residual errors (69 fishery, 45 pot survey, and 57 trawl survey) was calculated for male crab and 136 residual errors (60 pot survey and 76 trawl survey) were calculated for female crab, resulting in 216 degrees of freedom (d.f. = 171 + 136 − 53 − 14 − 24).

Our model was implemented in Microsoft Excel. Sensitivity analysis of selected parameter estimates, including natural mortality, was conducted by examining changes in model output parameters in response to alternative input parameters. To allow comparison among model configurations and to previous studies, we also included the following time series estimates of crab population stock status: (1) legal male abundance, the sum of legal-recruit and post-legal male crab; (2) mature female abundance, the sum of mature-recruit and post-mature female crab; and (3) sex ratio of reproductive crab, calculated as mature female abundance divided by model-estimated male total abundance. For simplicity in calculating the sex ratio, we considered all males to be functionally mature.

To examine variability in the estimated parameters, we used a bootstrap approach (Efron and Tibshirani, 1993) in which residuals are resampled with replacement and added to the predicted values, and the model re-run to obtain new parameter estimates. This process was replicated 1,000 times, with the standard deviations of the bootstrap parameters serving as estimates of the standard errors of the parameter estimates. Bootstrap results are given for male and female starting and annual recruit parameters, selectivity and catchability parameters, and annual natural and fishing moralities. Tabulated values are derived from the base model and include point estimates and the coefficients of variability, calculated as the standard deviations divided by the point estimates.

1.4 Results

1.4.1 Estimates of Male Abundance

Trends in the estimated absolute abundance for the modeled portion of the male crab population (i.e., male crab ≥125 mm CL) were generally consistent among different model configurations, although the absolute magnitude and timing of peaks in abundance differed slightly among different weightings of the input data. Under the base weighting scheme, total male abundance increased rapidly from 16.7 million crab in 1960 to peak abundance of 53.8 million crab in 1963, then declined rapidly to 7.8 million crab in 1969 (Fig. 1.4A). Estimated male abundance then oscillated on a 4–5-year period over the next 15 years, with peak abundances of 15.2 million crab in 1974 and 17.5 million crab in 1978, before falling to 0.7 million males in 1985. After 1985, estimated total male abundances fluctuated at levels generally less than 0.4 million crab.

Over the range of fixed mortality values considered, higher values of assumed natural mortality resulted in higher estimated total male abundances from the 1960s to the early 1980s (Fig. 1.4A). Although only M values of 0.1–0.4 are shown in Fig. 1.4A, the pattern was consistent across sexes and crab stage for all M values examined. Abundance estimates for the base weighting scheme were larger than estimates from fixed $M = 0.3$ and smaller than estimates from $M = 0.4$ in the mid 1960s and late 1970s, between abundances for $M = 0.2$ and $M = 0.3$ from the late 1960s to mid 1970s, and similar to

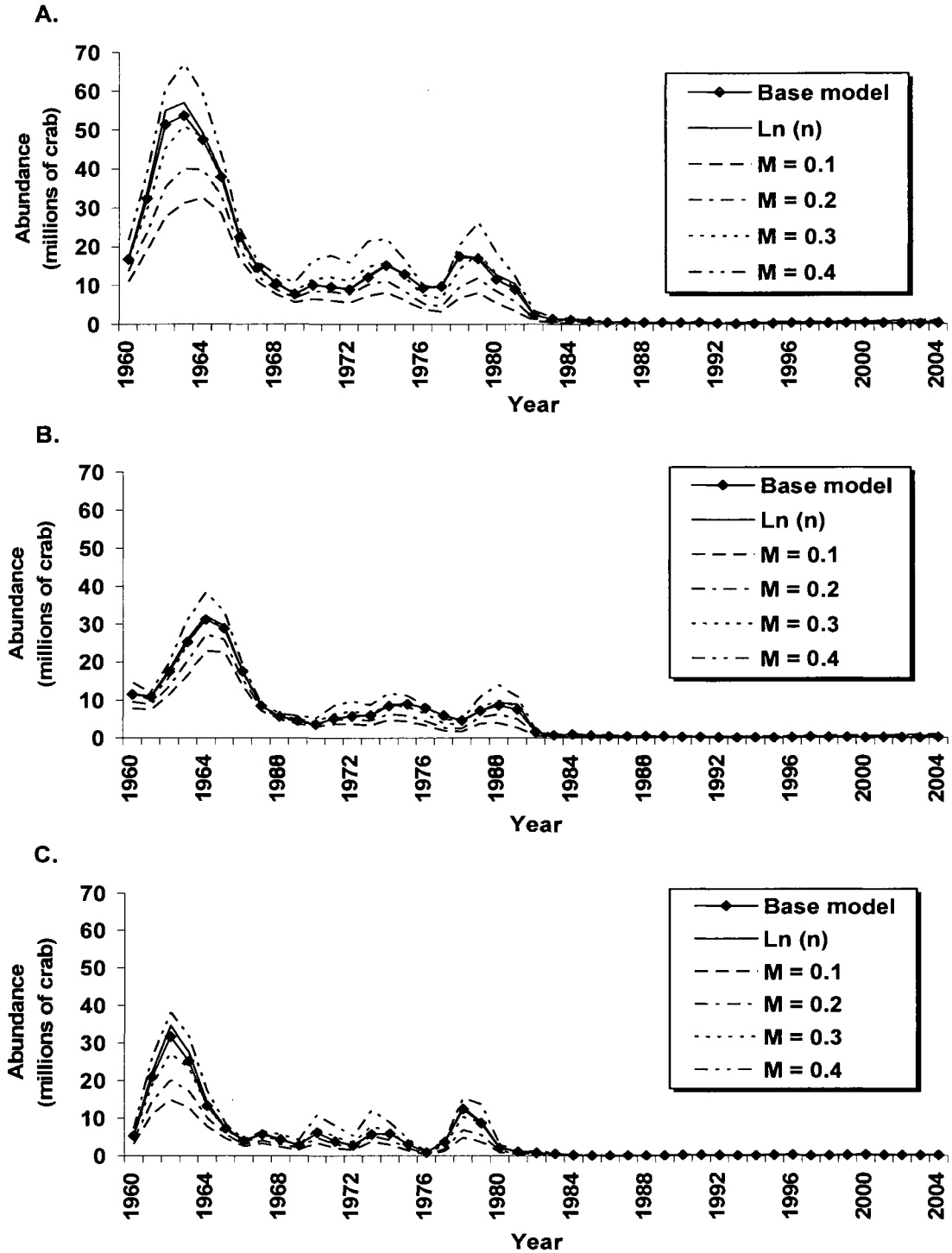

Figure 1.4. Estimated abundances of (A) all males, (B) legal males, and (C) male model recruits with data weighting according to the base model and the log of sample sizes under a natural mortality walk, and also under different fixed mortality schedules, 1960–2004.

estimates from $M = 0.3$ in the early 1980s. Otherwise, abundance estimates based on different fixed mortality schedules or weighting schemes, including those using logarithms of the sample size or increased weighting of individual datasets, were generally within 5% of the base configuration estimate for a given year (Figs. 1.4A–C and 1.5A–C). The primary exception was generally increased abundances during the peak years of 1960–1968 in association with a weighting of 5 or 10 applied to the fishery composition data or to the penalty for the random walk of fishing mortality. Patterns of estimated total abundances relative to dataset weighting and also to mortality weighting schemes were relatively consistent across components of the analyzed male population and will not be discussed further.

In the early portion of the time series for legal male crab, estimated abundances decreased slightly from 1960 to 1961 before increasing to peak abundance of 31.2 million crab in 1964 under the base weighting scheme (Fig. 1.4B). Abundance declined rapidly over the next few years to 8.5 million legal males in 1967, then fluctuated between 3.6 and 8.9 million crab through 1981. Abundance fell below 1.0 million crab beginning in 1983, and remained at low levels (median <0.2 million legal males) through the remainder of the time series.

Estimated male recruitment under the base weighting scheme increased from 5.4 million males in 1960 to a peak of 31.6 million males in 1962 (Fig. 1.4C). Recruitment declined rapidly over the next 3 years, and then fluctuated widely, between 0.9 and 12.4 million

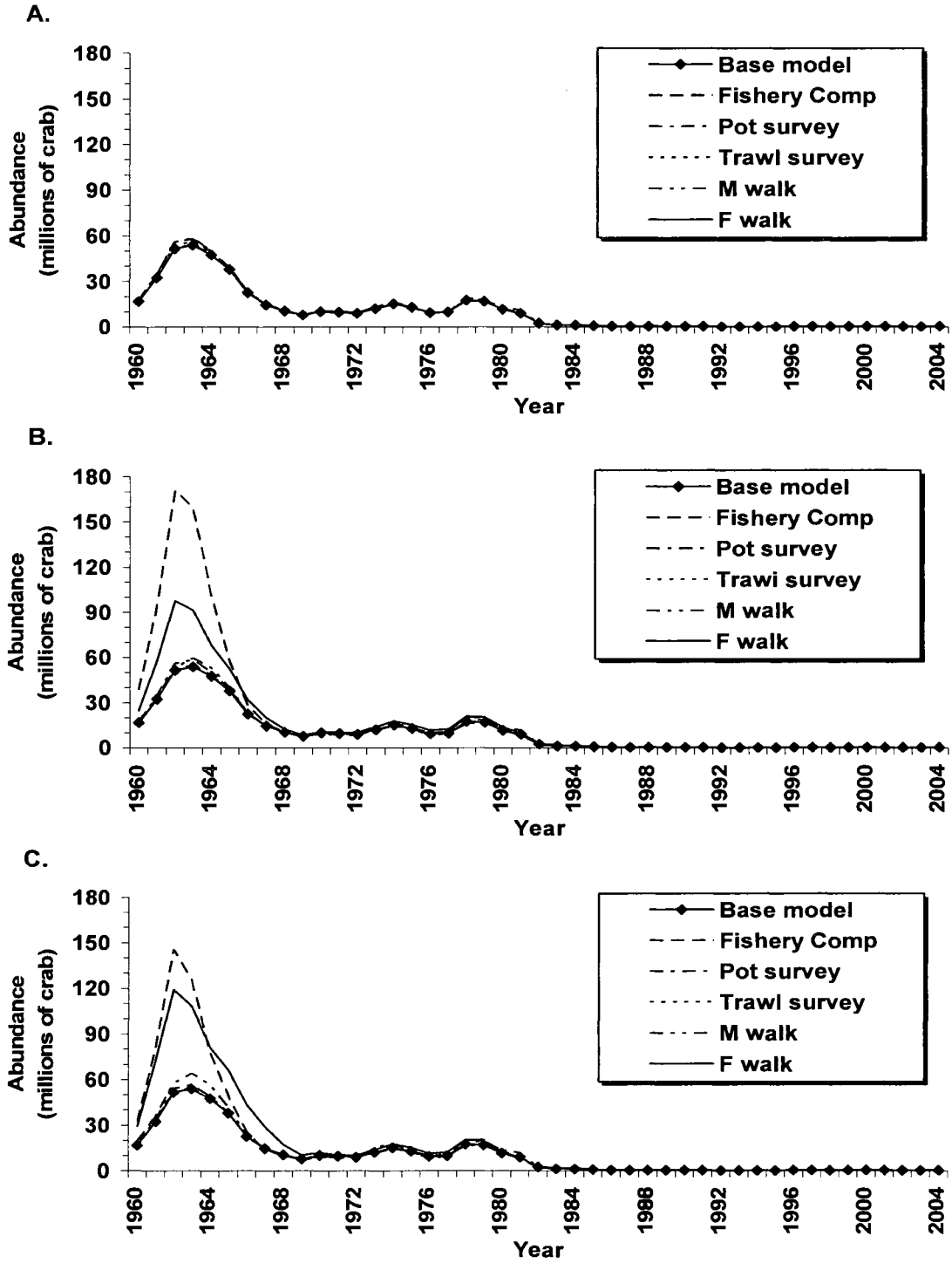

Figure 1.5. Estimates of total male abundance during 1960–2004 derived under the base model and under schemes in which all datasets receive unity weighting except for the single dataset as noted in which (A) $\lambda = 2$, (B) $\lambda = 5$, or (C) $\lambda = 10$.

crab, through 1981. Relatively low recruitment was estimated for the remainder of the time series, including virtual recruitment failures for some years, such as 1985–1989, and 1997; median recruitment after 1981 was estimated to be 0.1 million males. Based on the bootstrap analysis, the median coefficient of variation was 0.64 for male recruits among years (Table 1.2). Higher uncertainty was associated with years of lower abundance, particularly beginning in 1986 when the only available data were from the trawl survey.

Legal recruits, representing new molts into the legal male component of the population, are of critical importance to fishery managers as an index of stock status and presumed harvestable surplus to sustain the population over a series of fishing years. Estimates of legal recruits (not graphed here) under the base weighting scheme increased from 1.3 million crab in 1960 to peak abundance of 17.8 million recruits in 1963 and 16.8 million crab in 1964, followed by a rapid decline to 2.7 million crab in 1967. Abundance estimates then fluctuated from 1.2 to 5.3 million crab through 1981 before declining to generally <0.1 million legal recruits annually for the remainder of the time series. There was relatively low uncertainty (CV $\leq$ 0.21) associated with male selectivity parameters (Table 1.3) and with catchability parameters for the different survey gears, although variability for some parameters appears artificially low because the parameter was either fixed or constrained against an upper bound (e.g., 1.0) to improve model performance.

Table 1.2. Starting abundance and recruit estimates (thousands of crab) from the base model with bootstrapped coefficients of variation (CVs).

Parameter[a]	Value	CV	Parameter[a]	Value	CV
$Male_{PL,60}$	5,287	0.40	$I_{m,91}$	166	1.08
$Male_{LR,60}$	1,309	0.65	$I_{m,92}$	90	1.27
$Male_{PR,60}$	10,147	0.42	$I_{m,93}$	37	1.43
$I_{m,61}$	20,906	0.42	$I_{m,94}$	84	0.99
$I_{m,62}$	31,641	0.52	$I_{m,95}$	149	1.44
$I_{m,63}$	25,101	0.62	$I_{m,96}$	227	0.96
$I_{m,64}$	13,226	0.71	$I_{m,97}$	5	4.66
$I_{m,65}$	7,190	0.61	$I_{m,98}$	78	1.36
$I_{m,66}$	3,947	0.63	$I_{m,99}$	162	1.14
$I_{m,67}$	5,634	0.55	$I_{m,00}$	332	1.19
$I_{m,68}$	4,255	0.57	$I_{m,01}$	147	1.27
$I_{m,69}$	2,737	0.76	$I_{m,02}$	106	1.44
$I_{m,70}$	6,208	0.50	$I_{m,03}$	102	1.40
$I_{m,71}$	3,808	0.61	$I_{m,04}$	152	1.31
$I_{m,72}$	2,735	0.62	$Fem_{IS,72}$	7,209	0.75
$I_{m,73}$	5,684	0.53	$Fem_{MS,72}$	1,036	1.49
$I_{m,74}$	5,903	0.45	$Fem_{IL,72}$	455	0.96
$I_{m,75}$	3,072	0.53	$Fem_{ML,72}$	4,880	0.93
$I_{m,76}$	902	0.57	$I_{f,73}$	3,784	0.75
$I_{m,77}$	3,643	0.48	$I_{f,74}$	1,111	0.73
$I_{m,78}$	12,469	0.42	$I_{f,75}$	4,449	0.71
$I_{m,79}$	8,661	0.50	$I_{f,76}$	22,380	0.61
$I_{m,80}$	2,033	0.56	$I_{f,77}$	26,923	0.63
$I_{m,81}$	1,076	0.44	$I_{f,78}$	5,727	0.70
$I_{m,82}$	747	0.53	$I_{f,79}$	2,034	0.80
$I_{m,83}$	531	0.61	$I_{f,80}$	1,928	0.77
$I_{m,84}$	156	0.64	$I_{f,81}$	1,180	0.83
$I_{m,85}$	67	0.69	$I_{f,82}$	228	0.95
$I_{m,86}$	24	0.77	$I_{f,83}$	162	0.72
$I_{m,87}$	33	0.80	$I_{f,84}$	65	0.75
$I_{m,88}$	12	1.15	$I_{f,85}$	53	1.00
$I_{m,89}$	16	1.31	$I_{f,86}$	14	1.52
$I_{m,90}$	191	1.22	$I_{f,87}$	19	1.81

[a] Parameters are defined in the text.

Table 1.2. (continued)

Parameter[a]	Value	CV	Parameter[a]	Value	CV
$I_{f,88}$	429	1.53	$I_{f,97}$	390	1.52
$I_{f,89}$	525	1.49	$I_{f,98}$	1,622	1.54
$I_{f,90}$	572	1.57	$I_{f,99}$	1,024	1.44
$I_{f,91}$	332	1.42	$I_{f,00}$	678	2.54
$I_{f,92}$	245	1.66	$I_{f,01}$	918	1.53
$I_{f,93}$	623	1.69	$I_{f,02}$	503	2.51
$I_{f,94}$	804	1.59	$I_{f,03}$	918	0.91
$I_{f,95}$	6	9.49	$I_{f,04}$	918	0.91
$I_{f,96}$	139	1.98			

[a] Parameters are defined in the text.

Table 1.3. Estimates of catchability, selectivity, and natural and fishing mortality parameters from the base model with bootstrapped coefficients of variation (CVs).

Parameter[a]	Value	CV	Parameter[a]	Value	CV
q_P	0.0011	0.23	F_{70}	0.53	0.24
$s_{Mpre,P}$	0.8000	0.03	F_{71}	0.35	0.30
$s_{Mrec,P}$	1.0000	0.00	F_{72}	0.34	0.32
$s_{Mpos,P}$	1.0000	0.00	F_{73}	0.29	0.35
$s_{FImSm,P}$	0.1511	0.22	F_{74}	0.55	0.25
$s_{FMatSm,P}$	0.4303	0.24	F_{75}	0.45	0.29
$s_{FImLg,P}$	1.0000	0.00	F_{76}	0.38	0.33
$s_{FMatLg,P}$	1.0000	0.00	F_{77}	0.28	0.43
q_T	0.2438	0.45	F_{78}	0.28	0.42
$s_{Mpre,T}$	0.5909	0.21	F_{79}	0.35	0.34
$s_{Mrec,T}$	1.0000	0.00	F_{80}	0.17	0.49
$s_{Mpos,T}$	1.0000	0.00	F_{81}	1.26	0.14
$s_{FImSm,T}$	0.0200	0.24	F_{82}	1.76	0.16
$s_{FMatSm,T}$	0.0200	0.07	M_{60}	0.23	0.27
$s_{FImLg,T}$	0.6784	0.27	M_{61}	0.32	0.23
$s_{FMatLg,T}$	0.6784	0.29	M_{62}	0.41	0.20
$s_{Mpre,F}$	0.3733	0.12	M_{63}	0.38	0.22
$s_{Mrec,F}$	1.0000	0.00	M_{64}	0.29	0.27
$s_{Mpos,F}$	1.0000	0.00	M_{65}	0.29	0.31
$s_{FImSm,F}$	0.8000	0.13	M_{66}	0.34	0.31
$s_{FMatSm,F}$	0.8000	0.20	M_{67}	0.39	0.30
$s_{FImLg,F}$	1.0000	0.00	M_{68}	0.38	0.29
$s_{FMatLg,F}$	1.0000	0.00	M_{69}	0.36	0.28
F_{60}	0.21	0.40	M_{70}	0.32	0.28
F_{61}	0.41	0.24	M_{71}	0.23	0.35
F_{62}	0.39	0.23	M_{72}	0.10	1.39
F_{63}	0.13	0.35	M_{73}	0.10	1.15
F_{64}	0.20	0.34	M_{74}	0.11	0.94
F_{65}	0.55	0.21	M_{75}	0.10	0.93
F_{66}	0.75	0.16	M_{76}	0.10	1.21
F_{67}	0.78	0.15	M_{77}	0.48	0.40
F_{68}	0.61	0.22	M_{78}	0.65	0.30
F_{69}	0.51	0.26	M_{79}	0.39	0.51

[a] Parameters are defined in the text.

Table 1.3. (continued)

Parameter[a]	Value	CV	Parameter[a]	Value	CV
M_{80}	0.25	0.73	M_{92}	0.80	0.53
M_{81}	0.70	0.29	M_{93}	0.27	1.32
M_{82}	0.10	1.75	M_{94}	1.17	0.36
M_{83}	0.28	0.59	M_{95}	0.10	3.41
M_{84}	0.60	0.31	M_{96}	0.11	2.35
M_{85}	0.38	0.52	M_{97}	0.47	0.68
M_{86}	0.10	2.27	M_{98}	0.40	0.92
M_{87}	0.10	2.05	M_{99}	1.19	0.38
M_{88}	0.10	2.28	M_{00}	0.75	0.58
M_{89}	0.71	0.51	M_{01}	1.11	0.42
M_{90}	0.45	0.92	M_{02}	1.10	0.41
M_{91}	1.40	0.32	M_{03}	0.10	4.57

[a] Parameters are defined in the text.

1.4.2 Estimates of Female Abundance

General trends in estimated abundance of female red king crab considered in our model (i.e., females ≥88 mm CL) were similar across model configurations and also similar to male trends after 1971 when the estimates of male and female recruitment were linked in our model (Figs. 1.4A and 1.6A). Thus, both sexes exhibited a relative increase in abundance in the late 1970s before declining dramatically in the early 1980s. For the base weighting scheme with a random walk on natural mortality, total female abundance generally increased from 13.6 million female crab in 1972, the start of the female time series, to 52.1 million females in 1977 (Fig. 1.6A). Estimated abundance fell to 3.4 million females by 1982, and then fluctuated between 0.5 and 2.4 million crab through 2004. Different source data weighting and assumptions about natural mortality resulted in patterns of absolute abundance estimates that were generally similar to the patterns observed in male crab estimates, that is, increased natural mortality resulted in larger estimates of abundance during years of peak female abundances in the late 1970s (Fig. 1.6A). Slightly larger abundance estimates during these years were also associated with increased weighting of either the pot survey or the random walk of fishing mortality (Fig. 1.7A–C).

Estimated abundance of mature female crab under the base weighting scheme increased from 5.9 million in 1972 to 25.6 million in 1978, then steadily decreased to 1.8 million in

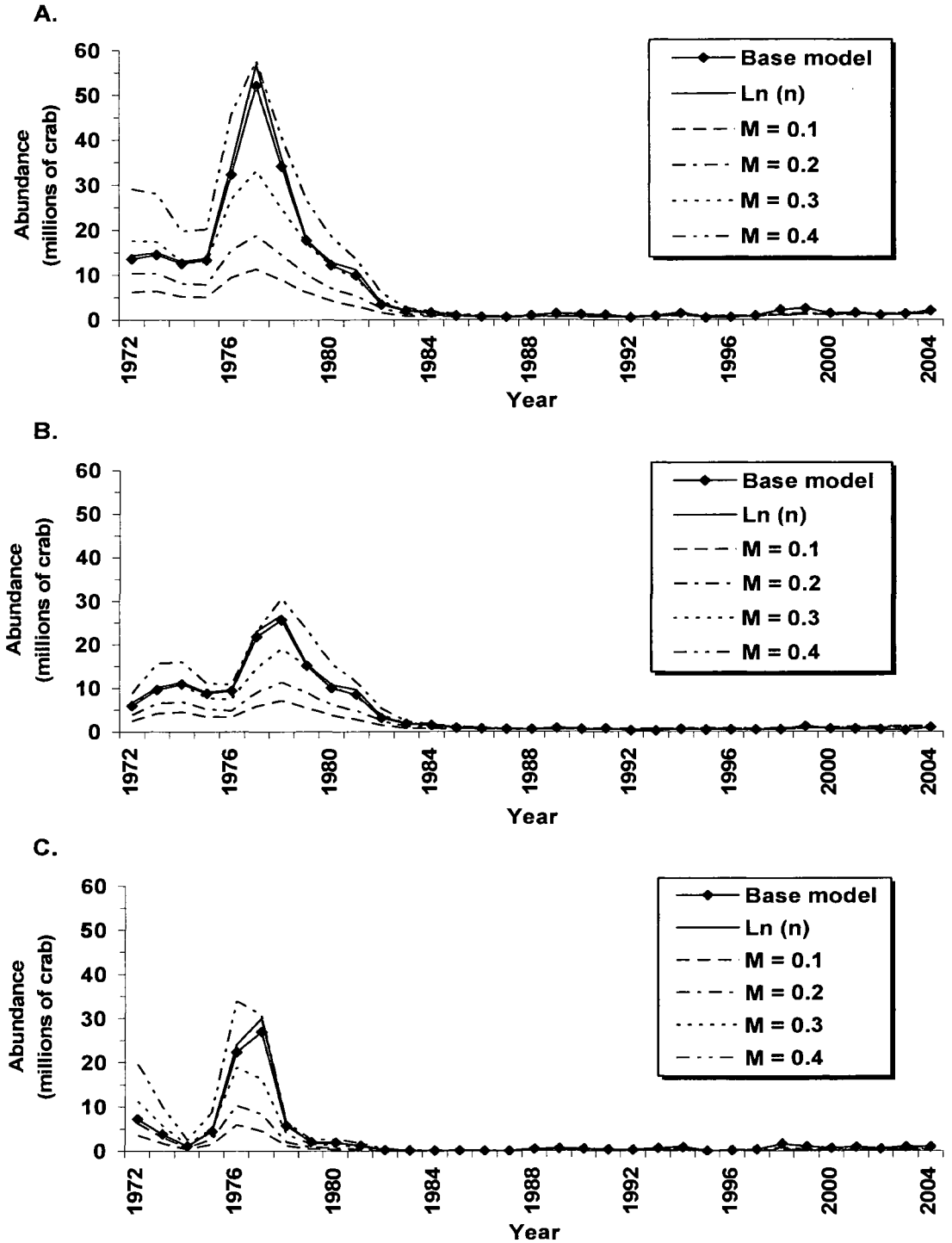

Figure 1.6. Estimated abundances of (A) all females, (B) mature females, and (C) female model recruits with data weighting according to the base model and the log of sample sizes under a natural mortality walk, and also under different fixed mortality schedules, 1972–2004.

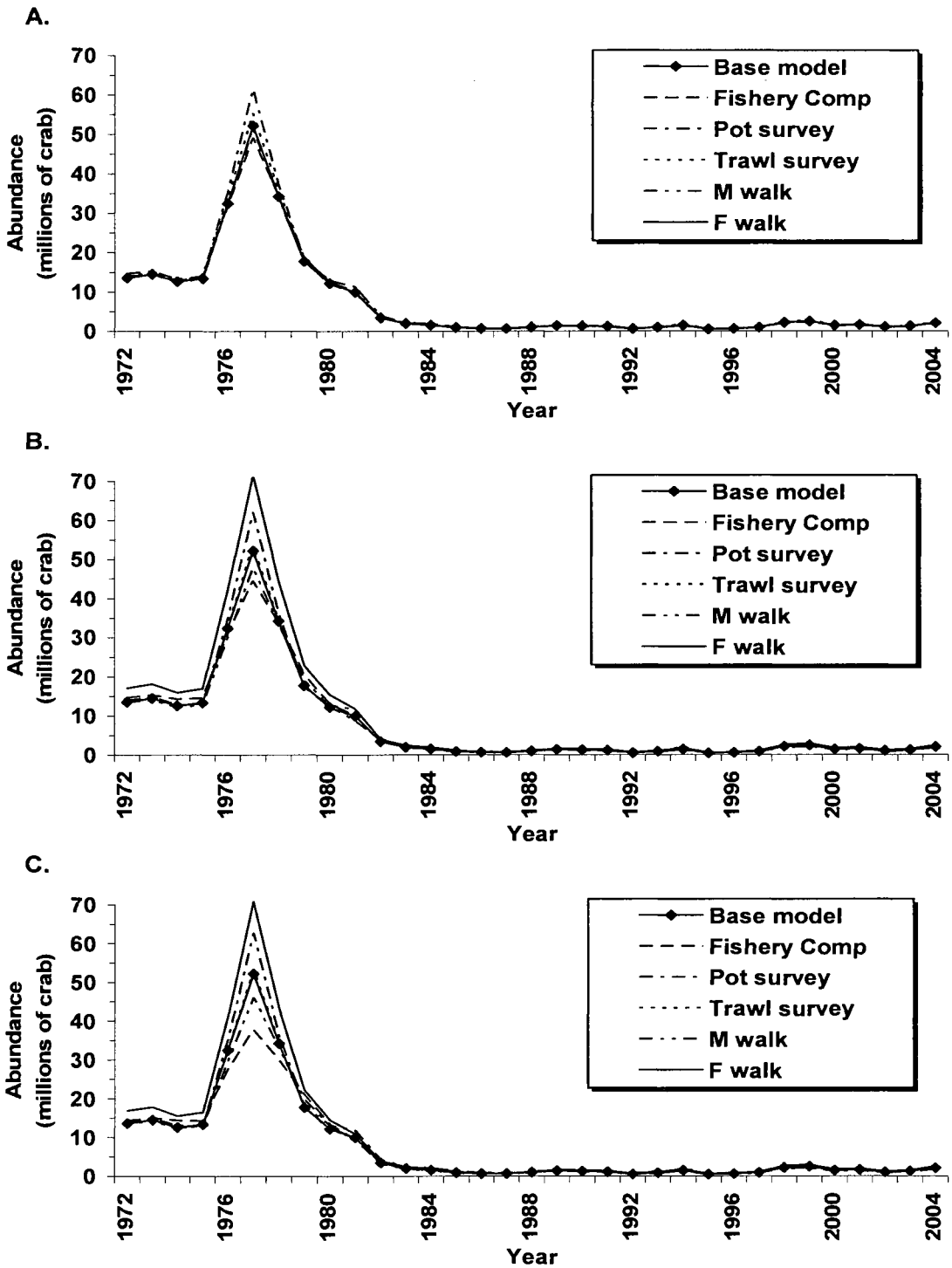

Figure 1.7. Estimates of total female abundance during 1972–2004 derived under the base del and under schemes in which all datasets receive unity weighting except for the single dataset as noted in which (A) $\lambda = 2$, (B) $\lambda = 5$, or (C) $\lambda = 10$.

1983 (Fig. 1.6B). Estimated abundances subsequently fluctuated at relative low levels between 0.2 and 1.5 million mature females (median = 0.6 million crab).

Estimated abundance of female recruits declined under the base weighting scheme from 7.2 million crab in 1972 to 1.1 million females in 1974, then increased to an estimated peak of 26.9 female recruits in 1977 (Fig. 1.6C). Estimated abundance declined drastically to 2.0 million female recruits in 1979 and subsequently fluctuated at levels generally less than 0.6 million recruits through the end of the time series. Similar to males, several virtual recruitment failures are indicated during this latter period, notably during 1984–1987 and 1995.

The coefficients of variation from the bootstrap analysis indicated substantial uncertainty in the estimates of female recruitment (median CV = 1.21; Table 1.2). Trends in uncertainty were similar to the patterns in male recruitment estimates; for example, higher uncertainty was associated with years of relatively low abundance, particularly with the data produced by the trawl survey beginning in 1986. However, the magnitude of coefficients of variability for female recruitment estimates were higher than those for the male recruitment estimates for a given time period (Table 1.2). There was relatively low uncertainty associated with female selectivity parameters (Table 1.3), although variability for some parameters appears artificially low because the parameter was either fixed or constrained against an upper bound (e.g., 1.0) to improve model performance.

1.4.3 Mortality and Sex Ratio

Model estimates of the rate of instantaneous fishing mortality, F, during the years 1960–1982 ranged from 0.13 to 1.76 for the base model (Table 1.3; Fig. 1.8A). In general, the lowest estimates of fishing mortality occurred in 1963 and 1964, during a strong pulse of recruitment and just prior to years of maximum harvest (Fig. 1.2 and Fig. 1.4). Other years of relatively low fishing mortality occurred in 1960, prior to full fishery development, and in 1971–1973 and 1977–1980, the latter being years of relatively low annual harvests when population abundance was declining (Fig. 1.2). Years of relatively high fishing mortality included 1961–1962, 1965–1970, 1974–1975, whereas very high F values occurred in 1981–1982, just prior to the fishery closure in 1983. Uncertainty in the estimates of fishing mortality was relatively low (median CV = 0.29; Table 1.3). The data weighting scheme had little effect on estimates of fishing mortality (data not graphed). However, a pattern of incrementally lower F associated with increased M under an assumption of constant natural mortality may suggest parameter confounding, particularly in the late 1970s (Fig. 1.8A).

Incorporation of a random walk into model estimation of natural mortality should provide a better fit to some of the data, but at a cost of an increased number of estimated parameters and potentially greater confounding among variables, as was mentioned above. General trends in abundance for the different crab stages were similar to those observed for model configurations with constant mortality assumptions (Fig. 1.4,

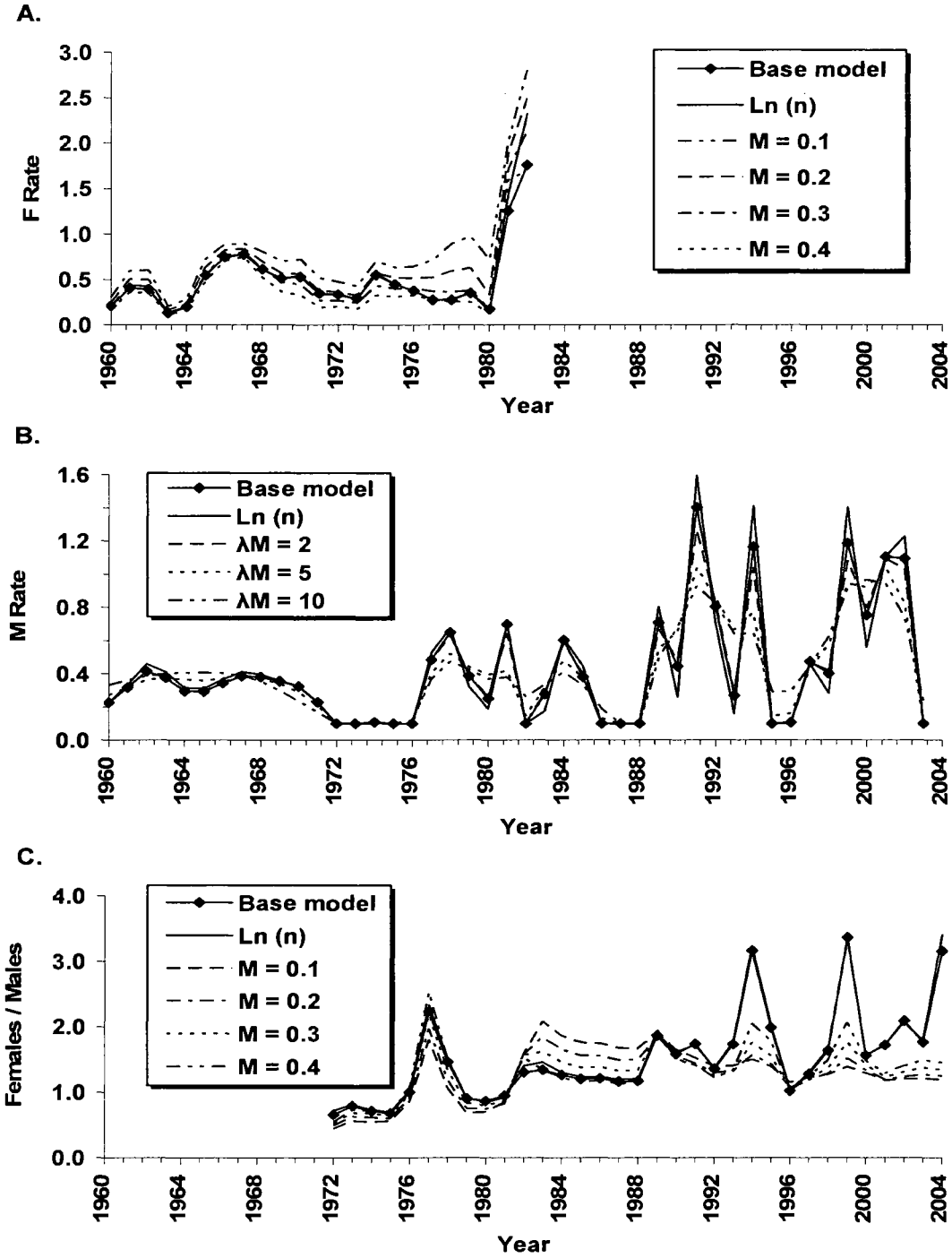

Figure 1.8. Estimates of (A) instantaneous fishing mortality on legal males ($F = 0$ after 1982), (B) natural mortality under a random walk, and (C) sex ratios of mature females to functionally mature males with data weighting relative to the base model over 1960–2004. Also shown are the effects of weighting by the log of sample sizes in all panels, different weights of the natural mortality walk in panel (B), and different fixed mortality schedules in panels A and C.

Fig. 1.5, Fig. 1.6, and Fig. 1.7). Estimates of natural mortality under a random walk approach were relatively stable through the 1960s, declined slightly in the mid 1970s, and generally increasing or relatively high beginning in the mid 1980s, although there was large interannual variability after 1976 (Table 1.3; Fig. 1.8B). Short periods of low natural mortality are suggested for 1972–1976, 1982, 1986–1988, 1995–1996, and 2003. In years where estimated M was bounded at a low level of 0.10, the bootstrap analysis indicated high uncertainty in the estimate.

Due to limitations in the time series of female data, the sex ratio prior to 1972 was not estimated. During 1972–2004, the ratio of mature females to total males under the base weighting scheme was quite variable (Fig. 1.8C). Overall, the ratio was near 1.0 during the first 4 years, increased during 1977 and 1978, returned to near unity during 1979–1981, reached a slightly higher, but stable level through 1988, after which substantial variability, ranging from 1.0 to 3.4, occurred through 2004. However, a generally increased sex ratio, suggesting more reproductive females than males, was indicated for the latter half of the time series. Model trends differed little as a result of alternative weighting configurations, as increased data weighting resulted in the sex ratio tracking closer to the base model (data not shown). Trends in the estimated sex ratios under assumptions of a constant natural mortality were generally similar to that of the base model, although ratios from constant mortality assumptions tended to exhibit less variability than the base model, particularly beginning in the mid 1990s (Fig. 1.8C).

1.5 Discussion

Our analysis was intended to provide an understanding of changes in red king crab abundance around Kodiak Island during a 45-year period from 1960 to 2004. Although indices of population status for this species were lacking prior to 1960, our analysis suggests that male crab abundance increased in the early 1960s, concurrent with the major expansion and development in the fishery and consistent with analysis by Rothschild et al. (1970). It is rather ironic that the increase in the population at this time helped fuel the expansion of this developing fishery to levels that apparently were not sustainable over the long term. The fishery became increasingly capitalized with the development of flowing seawater live tanks and the building of larger, full-time crab vessels capable of vastly increased fishing power. Increased crab abundance in the early 1960s was primarily driven by record crab recruitment to the pre-legal stage (Table 1.2; Fig. 1.4C). Concurrently, instantaneous fishing mortality on legal crab was relatively low in 1960, increased during 1961–1962, but was then outpaced in 1963–1964 by the increased abundance of crab molting into the legal size (Table 1.3; Fig. 1.4B). With the rapid expansion of the fishery in the mid 1960s, combined with technological changes that allowed the fleet to more efficiently harvest the available crab, fishing mortality rapidly increased to produce the record harvests of the 1964–1965 to 1967–1968 fishing seasons (Fig. 1.2). Instantaneous fishing mortality rates exceeded 0.55 in the mid to late 1960s as the fishery progressively expanded offshore (Table 1.3; Fig. 1.8A; Gray et al.,

1965). Over the next dozen years, the fishery was reduced to a recruit-driven fishery, evidenced by pulses of male recruitment on approximately a 4–5-year frequency that drove short-term increases in legal males, which was lagged somewhat by increases in harvests (Fig. 1.2 and Fig. 1.4B and 1.4C). As legal male abundance declined in the early 1980s, relative harvest rates increased. This was most pronounced in 1981 and 1982 when instantaneous fishing mortality rates exceeded 1.26, at the same time that annual harvests increased while legal male abundance declined to very low levels (Table 1.3; Fig. 1.2 and Fig. 1.4B). The failure of a subsequent recruitment pulse to appear, as had occurred in previous years, promoted the extremely high fishing mortality rate (Fig. 1.8A). That is, the harvest rate increased on a legal male population abundance that was rapidly decreasing. Despite the closure of the fishery since 1983, population abundance has failed to rebuild to previous levels. Generally high natural mortality levels since the early 1990s and skewed sex ratios since the late 1980s appear to have contributed to the continued lack of recovery (Fig. 1.8B and C). However, recent trends in sex ratio and estimated natural mortality should be interpreted cautiously because the trawl survey provides the only data after 1985, and recent survey data represent small sample sizes from a biased geographic coverage.

In a catch-length analysis of male red king crab abundance around Kodiak during 1964–1982, Zheng et al. (1996) estimated a peak abundance in the range of 25–39 million legal crab in the 1965 population, with the range in the estimates depending on the level of fixed natural mortality. Estimated legal abundances then fell to low levels in the late

1960s, recovering moderately in the early and mid 1970s before collapsing again after 1982. In their two-stage catch-survey analysis of Kodiak red king crab during 1973–1985, Collie and Kruse (1998) estimated that abundance of legal male crab peaked at approximately 9 million males in 1974, decreasing to 4 million males in 1978, followed by a slight increase to about 5 million males, before drastically falling to levels of less than 1 million males during 1983–1985. Thus, our estimated trend in legal male crab abundances was similar to the two previous studies. We note that our analysis indicated that legal male crab abundance was highest in 1964 (Fig. 1.4B), whereas Zheng et al. (1996) estimated the year of peak male abundance to be 1965. Although their results found a poor fit to 1964 carapace-length data, the discrepancy between studies may also relate to the time series and carapace lengths considered; Zheng et al. (1996) considered male crab ≥147 mm CL beginning in 1964, whereas our models consider male crab ≥125 mm CL beginning in 1960, thus utilizing additional data to estimate population trends.

Although all male red king crab considered in our analysis (i.e., ≥125 mm CL) were likely morphologically mature, the actual effectiveness at mating in a given year would have depended on the relative size distributions of mature males to mature females (Paul and Paul, 1990). Our results suggest that sex ratios derived from model estimates of population abundance became increasingly skewed toward females throughout the time series beginning in 1972 (Fig. 1.8C). This trend in increased sex ratios generally agrees with observations in the Kodiak pot survey, which found sex ratios increased from

~ 0.5:1.0 during 1973–1975 to ~ 2.2:1.0 in 1983 (Blau, 1986). Sex ratios were even more heavily skewed in favor of mature females in some bays studied during special research projects by ADF&G in the late 1960s (McMullen, 1968). In these bays many adult females, which should have been carrying egg clutches, were barren (McMullen, 1968), indicating that reproductive success was compromised. During the pot survey years, nearly all females had egg clutches that were 90–100% full during 1973–1975, but this declined through 1985 when only 15% had 90–100% clutch fullness (Becker et al., 1990). McMullen and Yoshihara (1969) suggested that high percentages of unmated female king crab in some Kodiak fishing districts in 1966–1967 were due to localized overharvest of mature males. This change in sex ratio in some embayments in the late 1960s occurred as the fishery spread progressively offshore in attempts to maintain catches despite warnings of overfishing at the time by some prominent scientists (e.g., Royce, 1969).

Despite the limitations of the trawl survey data, it is evident that the red king crab population has continued to remain at very low levels of abundance since the collapse of the population in the early 1980s. Although there are indications of periodic recruitment pulses, uncertainty is associated with these pulses. In addition, the application of a random walk to the mortality structure indicates a relatively high level of natural mortality occurring in two pulses. The first dramatic increase in the late 1970s to mid 1980s following a climate regime shift in 1976–1977 and a second increase appears to have followed a 1988–1989 regime shift (Fig. 1.8B). Indeed, the productivity of many

marine species seems to have been related to these decadal-scale climate shifts in the North Pacific (e.g., Beamish and Bouillon, 1993; Hollowed and Wooster, 1992; Hare and Mantua, 2000).

Like all modeling studies, there are caveats to our analysis. For instance, legal males should be the best estimated portion of the monitored population because data are available from both surveys and fishery removals. But, some errors occur when using the biological measurement CL to indicate legal crab size, which is based on CW for fishery management. Due to growth variability of individual crab, some males in our defined "pre-legal" stage actually have a legal carapace width, and visa-versa. Additionally, some harvests of sublegal males occurred because realistic enforcement of minimum legal size typically allows landings of a small proportion of sublegal crab (personal observation). Another complicating factor is that the minimum legal CW was not consistent among all years and fishery management subareas (Blau, 1988; Spalinger, 1992). Therefore, we used the crab stage definitions as a generalization for retrospective analyses with the recognition that deviations exist but are generally small and likely had little effect on our results. It is further recognized that our Monte Carlo approach to establish the growth matrix for the recursive equation (Eq. (1.2) does not allow for interannual changes to molt probabilities or growth rates in response to different environmental or ecological conditions. In Bristol Bay, periods of slow (1980–1984, 1992–1993), medium (1985-1991), and fast growth (1972–1979) were associated with shifts in molting probability over three decades (Balsiger, 1974; Zheng et al., 1995). However, our

approach uses the population size distribution during a period of relative high historical abundance (i.e., 1972–1986) to describe average growth characteristics across the entire time series, a conservative tact, so our assumption of fixed size classes may be reasonable.

Future analyses of Kodiak red king crab should focus on temporal changes in the stock biogeography with respect to oceanographic conditions, ecological factors, and historical harvests. Of particular interest is the relationship of red king crab abundance and recruitment to environmental and ecological factors, such as temperature effects on match–mismatch of crab larvae and their *Thalassiosira* prey, particularly given that larvae must feed within 2–6 days of hatching for optimal survival (Paul et al., 1989), and larval advection by currents to suitable nursery areas. Previous tagging and pen studies suggested that it takes 7–8 years for male red king crab in the Kodiak area to attain a legal size (McCaughran and Powell, 1977). In an exploratory analysis, we found negative correlations ($P \leq 0.05$) of red king crab recruitment with Kodiak air temperature (6–8-yr lags), water temperature (7-yr lag) at Trident Basin (an embayment on Kodiak Island), and the spring (6–8-yr lags) and annual (8–9-yr lags) Southern Oscillation Index.

Predation is also a likely cause for increased natural mortality during the latter portion of the time series examined here. In a similar study of the decline of the Kachemak Bay stock of northern shrimp *Pandalus borealis* a strong increasing trend in natural mortality, paralleling trends in increased Pacific cod *Gadus macrocephalus* abundance subsequent

to the 1976–1977 regime shift, was the most important factor controlling this stock during the late 1970s and early 1990s (Fu et al., 2000; Fu and Quinn, 2000). In the case of red king crab, first stage instars are likely highly susceptible to predation by a wide variety of shellfish and groundfish (e.g., Jewett, 1978; Jewett and Powell, 1979), including cannibalism (Broderson et al., 1990). However, field studies examining diets of likely predators have found little evidence of predation on any life stage of red king crab (Livingston, 1989; Dew and McConnaughey, 2005; Zheng and Kruse, 2006). Nevertheless, a cursory analysis of the ADF&G pot survey data revealed a strong increase in relative abundance of Pacific cod in nearshore waters around Kodiak at a time when the king crab population drastically declined. Potential relationships between Kodiak red king crab population dynamics and such environmental and ecological factors will be explored in a subsequent paper.

1.6 Conclusion

The rapid expansion of the red king crab fishery during the 1960s was associated with greater fishing capacity corresponding to increased participation by full-time crab fishing vessels. These vessels had flowing seawater live tanks and were capable of staying at sea for prolonged periods of time. As a coincidence, the 1960s expansion occurred during a period of record strong recruitment that sustained a growing fishery for a short period of time. Once recruitment declined in the late 1960s, exploitation rates escalated, sex ratios

became skewed toward mature females, and reproduction appears to have been compromised. In the 1970s, a few moderately strong year classes sustained the now recruit-driven fishery until the early 1980s, after which recruitment has failed for more than 20 years. Despite fishery closure since 1983, the stock has failed to recover. A climate regime shift in the late 1970s was associated with other ecosystem changes, including an increase in ocean temperatures and increases in the abundance of predatory fishes, such as Pacific cod. A second regime shift, in the late 1980s, exacerbated impacts to an already depressed crab stock. Given the lag difference between males and females from larval settlement to functional maturity, natural mortality likely has a greater effect on males and further skewed the sex ratio. The combination of low reproductive potential and unfavorable environmental conditions may have contributed to the longstanding depressed status of this stock.

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Chapter 2: Analysis of a Stock-Recruit Relationship for Red King Crab off Kodiak Island, Alaska[2]

2.1 Abstract

Waters of the northern Gulf of Alaska around Kodiak Island once supported the world's largest fishery for red king crab *Paralithodes camtschaticus*. Commercial fisheries began at low levels in the 1930s, increasing rapidly in the 1960s to a peak harvest of 42,800 mt in 1965. Stock abundance declined sharply in the late 1960s, moderated in the 1970s, and crashed in the early 1980s. A commercial fishery closure since 1983 has not resulted in stock recovery. To improve understanding of stock dynamics, we examined spawner-recruit (S-R) relationships for the Kodiak red king crab stock. The shape of the S-R relationship helps describe average stock productivity at different stock levels, thus relating directly to fishery management objectives. Due to limited female data, we used only male data and two currencies of male abundance as a proxy for spawners, either: (1) all males ≥ 125 mm carapace length (CL); or (2) legal males, (≥ 145 mm CL). Due to age uncertainty, we considered lag times of 5 to 8 years between reproduction and recruitment. Residuals from fitting a standard Ricker model were strongly negative for brood years from the mid 1970s to the mid 1980s and positive from the early to mid

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[2] Bechtol, W.R., and G.H. Kruse. *In press*. Analysis of a stock-recruit relationship for red king crab off Kodiak Island, Alaska. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science.

1990s. A Ricker model with autocorrelated errors resulted in better fits, with AIC_c values minimized for a 5-year lag using all males. Among model configurations, estimates of peak production ranged from 2.0 to 3.4 million recruits from a range of 11.3 to 37.7 million males. A model separating the time series into three productivity periods, corresponding to different ecological regimes, further improved model fit. Although abundances of both spawners and recruits have been < 1.0 million males since 1985, depensation at low stock sizes was not detected. Future analyses will examine the contribution of ecological and environmental factors to crab recruitment.

2.2 Introduction

The northern Gulf of Alaska near Kodiak Island (Figure 2.1) once supported the world's largest fishery for red king crab *Paralithodes camtschaticus*. Commercial harvests from this area first occurred in the 1930s, although annual harvests were relatively minor until the early 1960s when improved market conditions, changes in vessel technology, and the introduction of vessels designed specifically to harvest red king crab resulted in a rapid increase in fishing effort and catch (Figure 2.2; Gray et al. 1965; Spalinger 1992). Annual landings peaked at 42,800 t (94.4 million lb) in 1965, but despite much lower harvest levels in the 1970s (Figure 2.2; Spalinger and Jackson 1994), the population collapsed in 1982 (Table 2.1). A fishery closure in place since 1983 has failed to induce stock recovery.

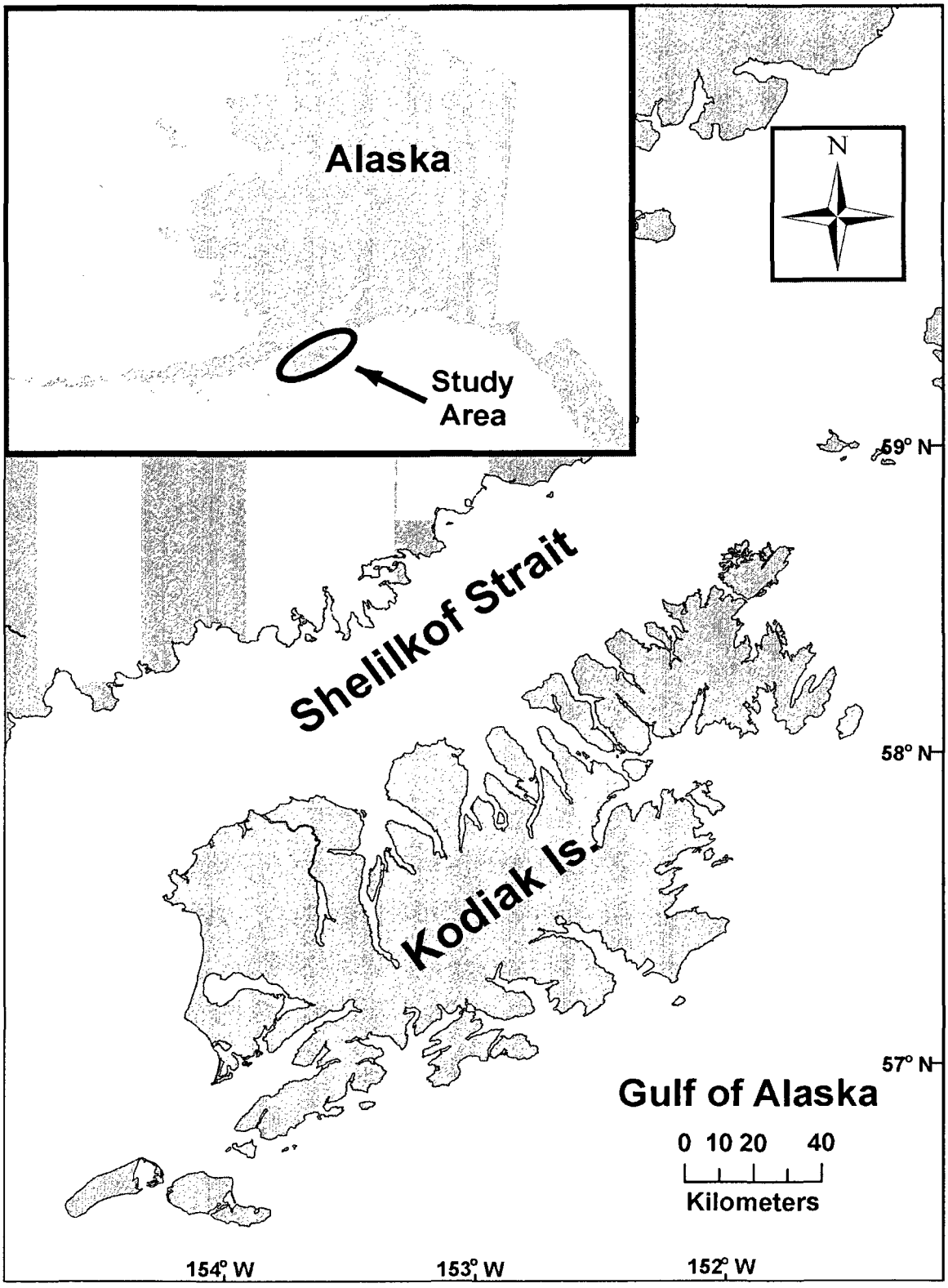


Figure 2.1. Study area around Kodiak Island, Alaska.

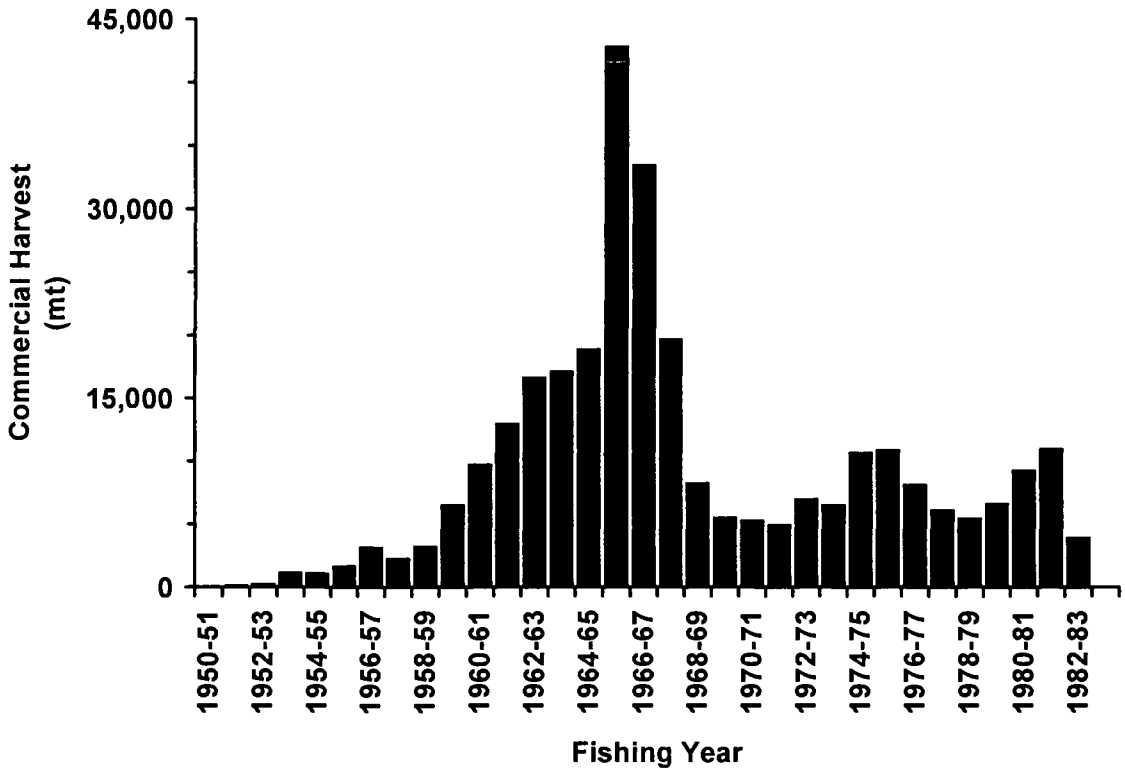


Figure 2.2. Annual harvests (mt) of red king crab from the Kodiak Management Area during 1950–1982.

Table 2.1. Annual estimated abundances (thousands of crab) of male model recruits, legal males, and all males for Kodiak red king crab, 1960-2004.

Year	Male recruits [a]	Legal males [a]	All males [a]
1960	5,287	11,456	16,743
1961	20,906	10,799	32,368
1962	31,641	17,415	51,435
1963	25,101	25,246	53,761
1964	13,226	31,176	47,523
1965	7,190	28,797	37,901
1966	3,947	17,552	22,500
1967	5,634	8,453	14,586
1968	4,255	5,662	10,508
1969	2,737	4,565	7,785
1970	6,208	3,628	10,171
1971	3,808	5,127	9,635
1972	2,735	5,696	8,980
1973	5,684	6,015	12,155
1974	5,903	8,458	15,220
1975	3,072	8,947	12,913
1976	902	7,930	9,371
1977	3,643	5,925	9,766
1978	12,469	4,646	17,481
1979	8,661	7,162	16,863
1980	2,033	8,575	11,615
1981	1,076	7,529	8,980
1982	747	1,552	2,394
1983	531	718	1,343
1984	156	940	1,173

Table 2.1. (continued)

Year	Male recruits [a]	Legal males [a]	All males [a]
1985	67	621	709
1986	24	474	509
1987	33	455	493
1988	12	440	458
1989	16	411	430
1990	191	210	403
1991	166	238	424
1992	90	97	194
1993	37	80	124
1994	84	89	178
1995	149	51	204
1996	227	162	412
1997	5	334	375
1998	78	229	311
1999	162	199	370
2000	332	105	445
2001	147	183	357
2002	106	109	224
2003	102	69	176
2004	152	144	312

[a] Male recruits are new recruit crab ≥ 125 and < 145 mm CL, legal males are crab ≥ 145 mm CL, and all males include all crab ≥ 125 ml CL; from Bechtol and Kruse (*in press*).

Recruitment is the primary determinant of dynamics of Alaskan crab populations (Zheng and Kruse 2000). To improve understanding of the role of population dynamics on the collapse and failure to recover of the Kodiak red king crab population, the goal of this study was to develop a spawner-recruit (S-R) relationship for this stock. The shape of the S-R relationship, which is a primary factor in determining average productivity at different stock levels, is an indicator of the potential role of recruitment overfishing on stock collapse and failure to recover and, thus, relates directly to fishery management objectives and the choice of harvest strategies to maintain a target level of stock production in the future.

Under the simplest approach, the S-R model assumes recruitment is related to stock biomass at low biomass levels, but density-dependent factors limit recruitment at high levels of stock abundance (Ricker 1975; Hilborn and Walters 1992; Quinn and Deriso 1999). In such cases, mortality during early life increases with increasing stock size, because survival becomes constrained by density dependence involving food, space, suitable habitat, or predators (Ricker 1954; Beverton and Holt 1957). If the early life stages are self-limiting, as might occur with competition for food or space, the S-R relationship might be described by a Beverton-Holt model, which approaches an asymptotic level of recruitment as stock abundance increases (Beverton and Holt 1957). In the Beverton-Holt model, compensation is assumed to occur throughout the range of stock sizes. However, many fished stocks exhibit overcompensation in which recruitment, representing spawning success over all life stages from reproduction to the

recruit stage, is a dome-shaped function that decreases as stock size increases beyond a peak production level, as in the Ricker S-R model.

Another consideration in S-R models is depensation, whereby per-capita production decreases disproportionately as stock size decreases at very low stock levels. Depensation may result from several sources including: reduced probability of fertilization; impaired group dynamics; reduced ability to condition the environment; or predator saturation (Allee et al. 1949; Liermann and Hilborn 2001). As an extension of this mechanism, population abundance may stabilize around a relatively low equilibrium, or predator pit (Peterman 1977).

The goal of our study was to determine if a biologically meaningful S-R relationship exists for Kodiak red king crab. Several Ricker S-R relationships warrant investigation. We first fitted the standard Ricker S-R relationship in which sequential observations are assumed to be independent and uncorrelated. However, autocorrelated environmental factors influencing crab recruitment may lead to strong serial correlation in recruitment such that good years tend to follow good years and poor years follow poor years (Quinn et al. 1990; Hare and Mantua 2000). Thus, as a second possibility, we applied an autocorrelated Ricker model in which errors in the S-R relationship are serially correlated. A third possibility, depensatory population dynamics (Quinn and Deriso 1999; Liermann and Hilborn 2001), may explain the continued low levels of abundance and recruitment for the Kodiak red king crab population beginning in the early 1980s. We

examined the potential of depensation by considering a gamma model, a three-parameter generalization of the Ricker (Reish et al. 1985). Zheng et al. (1995a, 1995b) similarly used depensatory and autocorrelated Ricker models to explore S-R relationships for Bristol Bay red king crab. The Bristol Bay models used female data from 1968 to the mid 1990s for recruitment and spawner biomass, but with spawners constrained by male reproductive potential. Subsequently, the S-R analysis for Bristol Bay was updated with a recruitment time series extending to 2001 (Zheng and Kruse 2003). Results of these efforts suggested an autocorrelated Ricker provided the best fit, although only marginally better than the depensatory model. Also, observed recruitment trends were consistent with decadal-scale climate shifts.

Because a lack of age structures prevents accurate age estimation of red king crab, the time lag between mating and subsequent model recruitment (specified below) must be specified. The consequence of uncertainty in this assumption was investigated by sensitivity analysis using a range of plausible time lags.

2.3 Methods

In a recent retrospective analysis (Bechtol and Kruse *in press*), we included data from dockside samples of commercial harvests (1960–1982) and indices of stock composition and relative abundance from pot (1972–1986) and bottom trawl surveys (1986–2004) in a

catch-survey analysis to yield estimates of crab abundance and recruitment. To maximize the available data for an S-R relationship, we limited our analysis herein to males because: (1) this is a male-only fishery (Pengilly and Schmidt 1995), so female abundance estimates were limited to survey years (1972–2004), whereas male estimates extended from 1960 to 2004 owing to availability of male commercial catch data; and (2) the years of highest population abundance, particularly the 1960s, are represented only by male data. Moreover, for consistency, male data were the basis of a recent analysis of S-R relationships for crabs in the eastern Bering Sea for purposes of revising overfishing definitions (NPFMC 2007).

In our previous analysis we defined three "stages" or classes of male crab: pre-legal, legal-recruit, and post-recruit (Bechtol and Kruse *in press*). The minimum size limit for legal retention of male red king crab for most years in the Kodiak Management Area was 178 mm carapace width, equivalent to ~145 mm carapace length (CL; Blau 1988). The growth increment of adult males at this size is approximately 20 mm CL (McCaughran and Powell 1977). So, we defined legal-recruits as newshell males $\geq$ 145 mm CL and $<$ 165 mm CL, i.e., determined to have molted to a legal size within the previous year. Post-recruit males were defined as having been legal size for at least one year and included oldshell and very oldshell males that are $\geq$ 145 mm CL and $<$ 165 mm CL, plus all males $\geq$ 165 mm CL regardless of shell condition. Pre-legal crab are considered to be one molt smaller than legal size and were defined as males of any shell condition that are $\geq$ 125 mm CL and $<$ 145 mm CL. Given the available data, we defined recruitment as the

number of crab in the pre-legal stage entering the modeled population rather than those entering the fishery or to some earlier life stage (e.g., larval settlement into the benthos). In the Kodiak area, male size at physiological maturity (75 to 85 mm CL), the size at which sperm are produced, is smaller than size at functional maturity (≥ 130 mm CL), the size at which males have been observed in mating pairs. Mean age for male functional maturity was believed to be 7 to 8 years (McCaughran and Powell 1977). Male crab can copulate with multiple females during the mating season, but laboratory studies found reduced fertilization success associated with smaller males and with secondary or later matings by a given male (Paul and Paul 1990; Paul and Paul 1997). In the wild, mating success with multiple females may be further constrained by factors such as the availability of mates, duration of pre-mating and post-mating male attendance, synchrony of female molting, and the relatively short duration of the mating season. Thus, much uncertainty exists concerning the component of the assessed male population in a given year that may have contributed to future recruitment. Given this uncertainty, we examined the sensitivity of our assumptions about the reproducing male population in two ways. First, we considered plausible time lags ranging from 5 to 8 years between the year of reproduction, or brood year, and the year of recruitment to the assessment model. Second, we examined two definitions of the reproducing male population which we refer to as "currencies." This approach was needed because, in contrast to the crab fishery which is managed based on a knife-edged delineation of legal size, sexual maturation in male red king crab occurs across a relatively broad range of sizes. However, the contribution of different size components of the male population to reproductive success

varies according to the size composition of the female component of the population (Paul and Paul 1990; Kruse 1993; Paul and Paul 1997); the relative male and female compositions change according to year class strength due to differential male and female growth rates (McCaughran and Powell 1977). To address uncertainty in male reproductive contribution across long-term population patterns, we considered male spawner currencies as including either: (1) all male crab ≥ 125 mm CL; or (2) only the legal-recruit and post-legal stages, i.e. males ≥ 145 mm CL.

The relationship between recruitment and the estimated reproductive stock abundance was examined with the Ricker model (Ricker 1954),

$$R_t = \alpha S_{t-k} e^{-\beta S_{t-k} + v_t} \quad , \tag{2.1}$$

where α is a productivity parameter representing production at low stock size, β is a parameter controlling the degree of density dependence, R is recruit abundance in year t, S is stock size lagged k years from year t, and v_t is unexplained variation. By letting $v_t = \delta_t + \varphi v_{t-1}$ where δ_t is environmental white noise, assumed be distributed as $N(0,\sigma^2)$, Equation 2.1 incorporates autocorrelation effects with φ representing the degree of autocorrelation among residuals in the predicted relationship. Setting $\varphi = 0$ results in the standard Ricker. The depensatory model is given by:

$$R_t = \alpha S_{t-k}^{\gamma} e^{-\beta S_{t-k}+\nu_t} = \alpha S_{t-k}\left(S_{t-k}^{\gamma-1} e^{-\beta S_{t-k}+\nu_t}\right) , \tag{2.2}$$

where $\gamma > 1$ suggests depensation and other parameters are as in Equation 2.1, including configurations with and without autocorrelation (Reish et al. 1985; Quinn and Deriso 1999).

These equations were linearized by taking logarithms:

$$\begin{aligned} \ln\left(\frac{R_t}{S_{t-k}}\right) &= \ln(\alpha) - \beta S_{t-k} + \nu_t \\ \ln\left(\frac{R_t}{S_{t-k}}\right) &= \ln(\alpha) + (\gamma - 1)\ln\left(S_{t-k}\right) - \beta S_{t-k} + \nu_t . \end{aligned} \tag{2.3}$$

Peak recruitment in the Ricker model occurs at a stock size (S_p) of $1/\beta$, and in the depensatory model at a stock level of γ/β, provided that $\gamma > 0$ and $\beta > 0$. The presence of autocorrelation was tested by calculating the lag-1 Pearson correlation of the residuals from the model and applying the standard hypothesis test of zero correlation (Zar 1999). Per-capita productivity and depensation among competing models was compared using α and β, respectively, divided by peak spawner abundance (S_p), so that comparisons between the two male currencies could be made.

To explore whether there were climate regime changes in the S-R parameters, we further evaluated our optimal models using configurations with up to three of each of the α and β parameters across the 45-year time series. The sequence of years chosen for a given α and β parameter combination was examined through trial and error by iteratively adjusting the transition points, but beginning with those years that were previously identified as being ecosystem regime shifts (Hare and Mantua 2000; Peterman et al. 2000).

These models were implemented in AD Model Builder (Otter Research Ltd., Sidney, B.C., Canada), with additional validation using Microsoft Excel (Microsoft Corporation, Redmond, Washington). Relative precision of an estimated parameter was reported as the coefficient of variation *(CV)*, the standard error (obtained in AD Model Builder) divided by the estimate.

In addition to visual examination of residual patterns, our approach to model selection involved comparing AIC_c values (Burnham and Anderson 2004):

$$\hat{\sigma} = \sqrt{\frac{RSS}{n-p}}$$

$$-2\ln L = n\ln\left(2\pi\hat{\sigma}^2\right) + \frac{RSS}{\hat{\sigma}^2} \qquad (2.4)$$

$$AIC_c = -2\ln L + 2p + \frac{2p(p+1)}{n-p-1}$$

where n is the number of observations, RSS is the residual sums of squares, p is the number of parameters in the model, and AIC_c is a formulation of the Akaike Information Criterion corrected to accommodate small sample sizes (n). According to Burnham and Anderson (2004), no credible evidence exists to eliminate competing models with AIC_c differences of ≤ 2, weak evidence exists for elimination with differences of 2 to 4, and definite evidence exists for differences ≥ 4. To provide comparable results among configurations, recruit abundances resulting from the 1960 to 1996 brood years were examined, giving $n = 37$ observations for reproduction to recruitment lags of 5 to 8 years.

Several alternative models were also examined, including the Beverton-Holt (Beverton and Holt 1957), Ludwig-Walters (Ludwig and Walters 1989), Deriso-Schnute (Deriso 1980; Schnute 1985); and Shepherd (Shepherd 1982). Results of the Beverton-Holt model were similar to results of the Ricker model and are not presented. The other models were less parsimonious based on AIC_c values and residual patterns and are excluded from further discussion.

2.4 Results

Estimated recruitment abundance was highly variable over time (Table 2.1; Bechtol and Kruse *in press*), with a ratio of strongest to weakest recruitments of 6,328 (31.6 million male crab in 1962 versus 5.0 thousand male crab in 1988). However, given the time lag

between mating and recruitment, the S-R analysis excluded the years of highest recruitment in the early 1960s because stock abundance estimates were not available for the associated brood years in the 1950s. Within the range of recruitments beginning in 1965, giving a minimum lag of five years corresponding to the smallest lag reported here, the ratio became 2,494 between the strongest (12.5 million males in 1978) and weakest (5.0 thousand males in 1988) recruitments. Observed recruitment was highest in the 1960s, moderate in the late 1960s and 1970s, and weak from the mid 1980s to the present (Table 2.1). Years of high recruitment were associated with moderate to high spawning stock abundances in the 1960s and early 1970s, whereas both recruitment and estimated male reproductive abundance have remained low since 1982.

Estimated peak recruitment among standard Ricker curves ranged from 1.9 to 4.5 million male crab (Table 2.2). Peak recruitment was inversely related to the lag length between brood year and recruitment. Spawner abundance corresponding with peak recruitment ranged from 24.2 to 44.0 million crab if measured as legal males ($\geq$ 145 mm CL), or 42.4 to 81.3 million crab if measured as all males ($\geq$ 125 mm CL; Table 2.2). However, this spawner abundance level is well beyond the observations for all brood years (Figures 2.3a, 2.3c, 2.3e, and 2.3g). The S-R relationships for brood years after 1982 reveal a very different relationship between recruitment and spawner abundance owing to the sharp reduction in male abundance and recruitment levels beginning in the early 1980s (Figure 2.4). Estimates of α and β were larger for models based on legal-male rather than all-male

Table 2.2. Parameter estimates and their standard deviations, and corresponding estimates of peak abundances of male spawners and model recruits for the standard Ricker and autocorrelated Ricker models.

	Parameter estimates and standard deviations [a]						Peak abundances (x 1,000 crab)	
	α		β		Φ			
Model[a]	Est.	CV	Est.	CV	Est.	CV	Spawners	Recruits
Standard Ricker								
5L	0.26	0.15	2.3 x 10-05	0.64	NA	NA	44,016	4,209
6L	0.24	0.15	2.9 x 10-05	0.39	NA	NA	34,256	3,052
7L	0.23	0.15	3.6 x 10-05	0.41	NA	NA	28,140	2,369
8L	0.22	0.15	4.1 x 10-05	0.35	NA	NA	24,237	1,923
5A	0.15	0.15	1.2 x 10-05	0.65	NA	NA	81,273	4,503
6A	0.14	0.15	1.8 x 10-05	0.45	NA	NA	56,959	3,001
7A	0.14	0.15	2.2 x 10-05	0.37	NA	NA	46,445	2,325
8A	0.13	0.15	2.4 x 10-05	0.34	NA	NA	42,355	1,972
Autocorrelated Ricker								
5L	0.49	0.52	6.3 x 10-05	0.53	0.75	0.10	15,939	2,890
6L	0.39	0.50	6.1 x 10-05	0.54	0.76	0.09	16,499	2,350
7L	0.54	0.64	7.9 x 10-05	0.43	0.82	0.08	12,589	2,498
8L	0.48	0.58	8.9 x 10-05	0.38	0.80	0.08	11,263	1,988
5A	0.24	0.48	2.7 x 10-05	0.70	0.73	0.11	37,726	3,354
6A	0.23	0.48	3.8 x 10-05	0.50	0.75	0.09	26,361	2,222
7A	0.30	0.59	4.9 x 10-05	0.40	0.80	0.09	20,205	2,258
8A	0.25	0.56	4.2 x 10-05	0.46	0.80	0.08	23,871	2,154

[a] The number in the model name identifies the lag in years between brood year and model recruitment, "A" implies all males and "L" implies legal males only, "Est." is the parameter estimate, "CV" is the coefficient of variation of the estimate, and NA is not applicable.

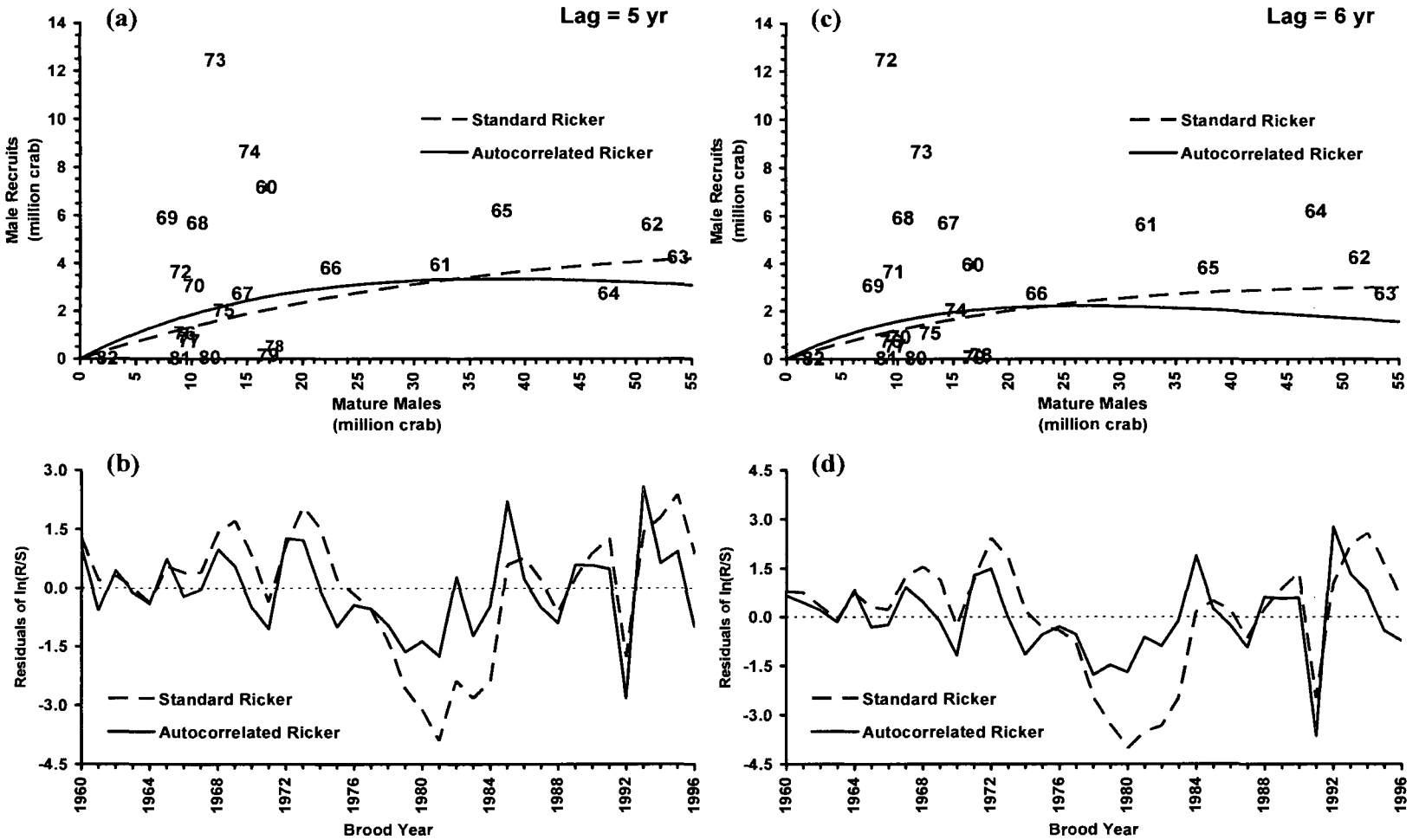


Figure 2.3. Standard Ricker (dashed line) and autocorrelated Ricker (solid line) curves with 5–8 year lags showing male recruits and all male abundances (upper panels), and prediction residuals by brood year (lower panels), for the1960–1996 brood years. Numerical labels on upper panels indicate the 1960–1996 brood years.

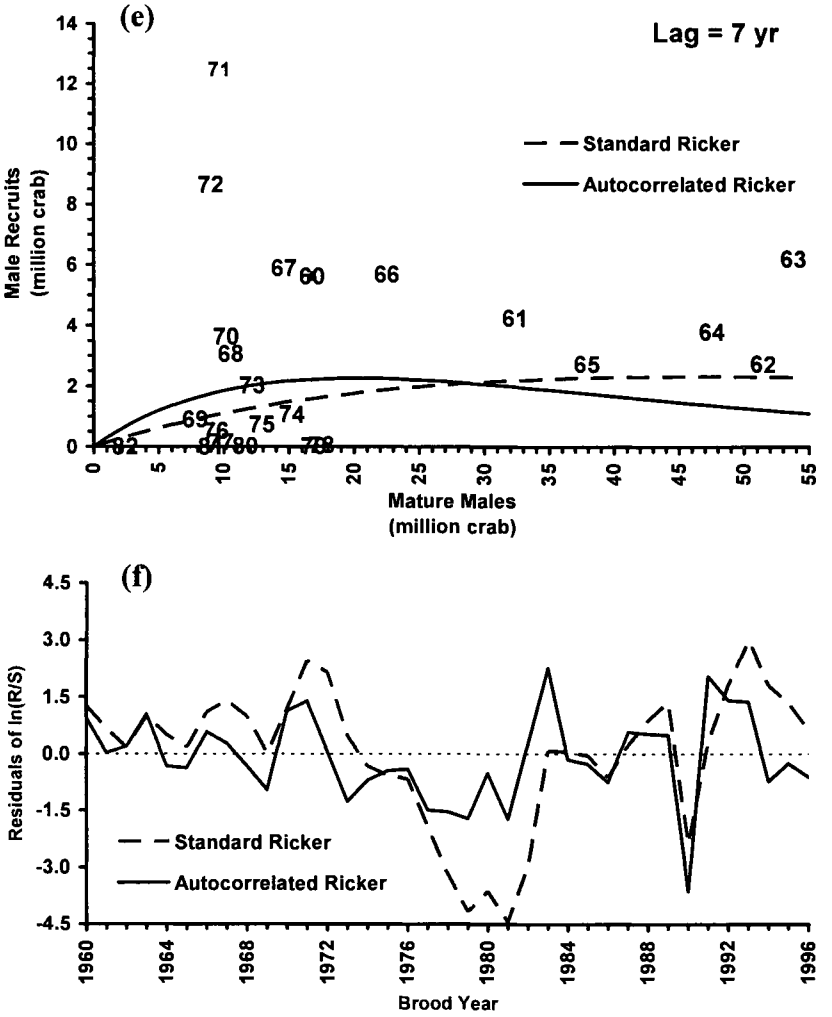
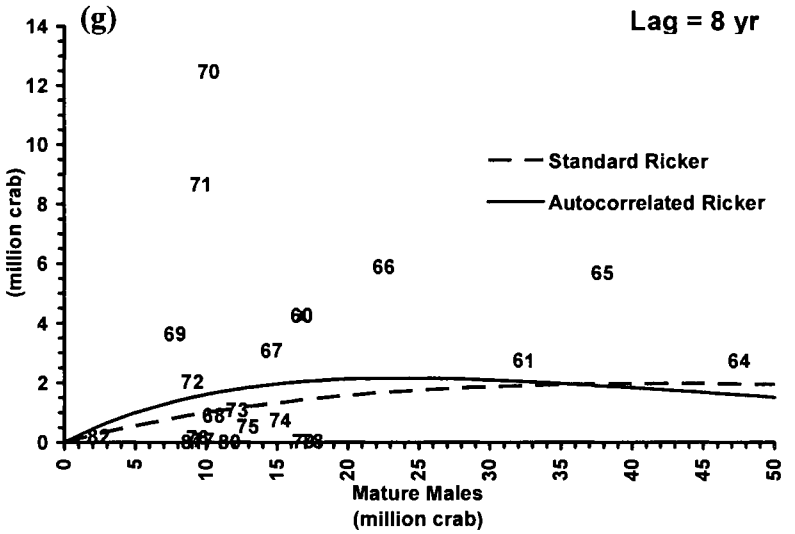
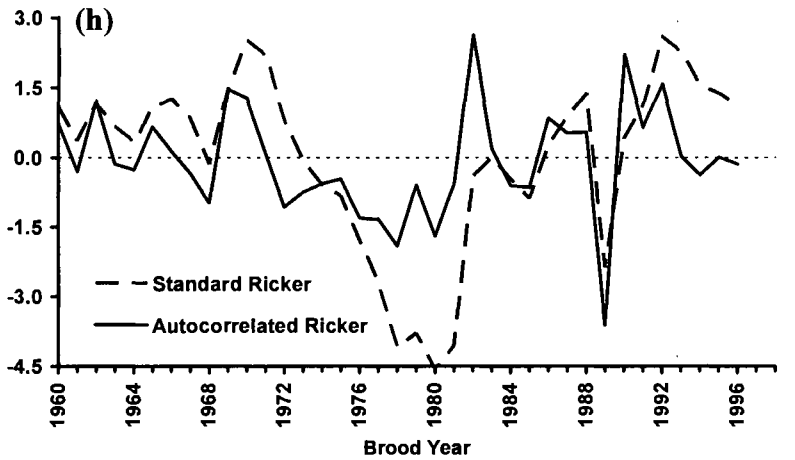


Fig. 2.3. (continued)


(g)
Lag = 8 yr
(million crab)
Standard Ricker
Autocorrelated Ricker
Mature Males
(million crab)


(h)
Standard Ricker
Autocorrelated Ricker
Brood Year

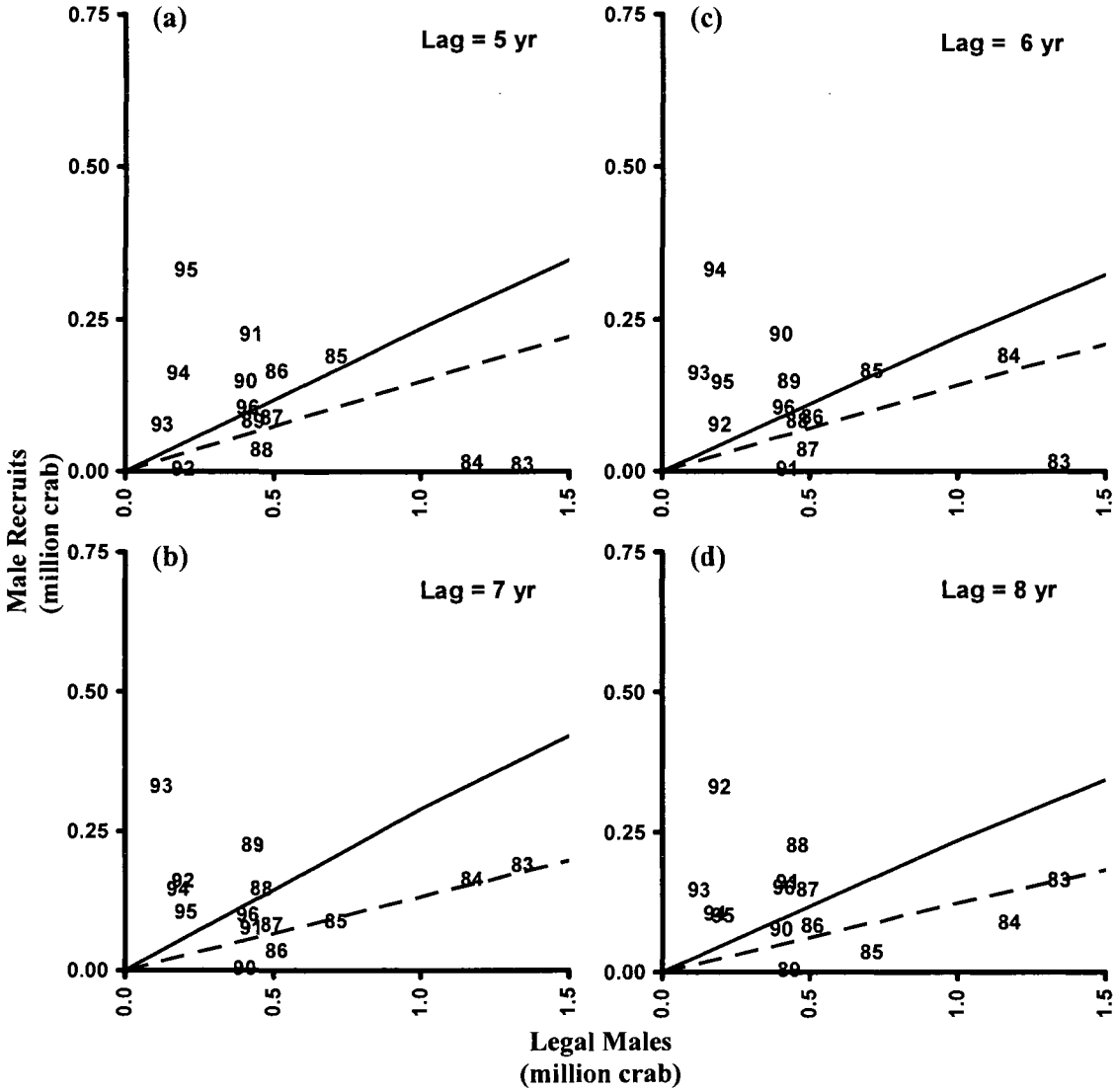


Figure 2.4. Origin area of the standard Ricker (dashed line) and autocorrelated Ricker (solid line) curves with 5–8 year lags showing male recruits and all male abundances for brood years after 1982. Numerical labels are brood years.

models under similar lags and correlation configurations (including for autocorrelated models discussed below), although the precision of the estimates was similar for a given configuration (Table 2.2). For all lag times examined with the standard Ricker models, residuals were distributed around zero during the 1960s, moderately to strongly positive during the early 1970s and mid 1990s, and strongly negative from the late 1970s to early 1980s (Figures 2.3b, 2.3d, 2.3f, and 2.3h). All models showed a strongly negative residual associated with the 1997 recruits, regardless of the brood year. Model fit, indicated by larger AIC_c values, generally decreased with longer recruitment lags and fits were better for an all-male currency compared to a legal male currency. Among standard Ricker models, the optimal configuration was a 5-year lag using an all-male currency based on an AIC_c value of 141.5 (Table 2.3).

Results of the test of serial correlation were highly significant ($P << 0.01$) for the model residuals from all standard Ricker models but not significant for residuals from all autocorrelated Ricker models (results not tabulated). A similar result was obtained for the depensatory models with and without an autocorrelation parameter. This indicates a bias in the results of the standard models because the assumption that data are uncorrelated is violated. The autocorrelation parameter corrects for this bias.

For a given male currency and recruitment lag, incorporation of autocorrelation into the Ricker models reduced the spawner abundance estimated to produce peak recruitment (Table 2.2; Figures 2.3a, 2.3c, 2.3e, and 2.3g). Peak recruitment under the autocorrelated

Table 2.3. Numbers of parameters, and estimated RSS, AIC_c, and per-capita productivity values for each configuration of the standard Ricker and autocorrelated Ricker models.

Model [a]	p	RSS	AIC_c	α/S_p	β/S_p
		Standard Ricker			
5L	2	98.4	145.6	5.9×10^{-06}	5.2×10^{-10}
6L	2	106.8	148.6	1.0×10^{-05}	1.4×10^{-09}
7L	2	124.9	154.4	8.1×10^{-06}	1.3×10^{-09}
8L	2	137.6	158.0	8.9×10^{-06}	1.7×10^{-09}
5A	2	88.0	141.5	1.9×10^{-06}	1.5×10^{-10}
6A	2	106.8	148.6	2.5×10^{-06}	3.1×10^{-10}
7A	2	120.5	153.1	2.9×10^{-06}	4.6×10^{-10}
8A	2	128.8	155.6	3.0×10^{-06}	5.6×10^{-10}
		Autocorrelated Ricker			
5L	3	46.6	120.4	3.1×10^{-05}	3.9×10^{-09}
6L	3	49.2	122.4	2.3×10^{-05}	3.7×10^{-09}
7L	3	46.8	120.5	4.3×10^{-05}	6.3×10^{-09}
8L	3	55.0	126.5	4.3×10^{-05}	7.9×10^{-09}
5A	3	43.7	118.0	6.4×10^{-06}	7.0×10^{-10}
6A	3	49.1	122.4	8.7×10^{-06}	1.4×10^{-09}
7A	3	49.2	122.4	1.5×10^{-05}	2.4×10^{-09}
8A	3	50.2	123.2	1.0×10^{-05}	1.8×10^{-09}

[a] The number in the model name identifies the lag in years between brood year and model recruitment, "A" implies all males, and "L" implies legal males only; RSS is the residual sums of squares, α is the productivity, β is density-dependence, and S_p is peak spawner abundance.

Ricker ranged from 2.0 to 3.4 million males resulting from a range in spawner abundance of 11.3 to 16.5 million crab if measured as legal males, or 20.2 to 37.7 million crab if measured as all males (Table 2.2). The autocorrelated models had higher per-capita productivity (α/S_p) and greater density dependence (β/S_p,) than comparable standard Ricker models (Table 2.3). As a result, the autocorrelated models estimated greater productivity than the standard Ricker models at low to moderate spawner abundances (Figures 2.3a, 2.3c, 2.3e, 2.3g and 2.4a-d). However, there was greater uncertainty in the estimated parameters for the autocorrelated Ricker models (CVs ranged from 0.48 to 0.64 for α and from 0.38 to 0.70 for β) relative to the estimates for the standard Ricker models (the CV was 0.15 for α and from 0.34 to 0.65 for β). Improved model fit, as indicated by smaller AIC_c values, was obtained for the autocorrelated Ricker models compared to the standard Ricker models (Table 2.3). Improved model fit for all-male currencies was less pronounced for the autocorrelated models with longer recruitment lags. Residuals were generally smaller (i.e., closer to 0) for the autocorrelated Ricker compared to the standard Ricker during many years, particularly years in which the largest residuals were observed, such as during the late 1970s to early 1980s (Figures 2.3b, 2.3d, 2.3f, and 2.3h). Regardless of the brood year, all autocorrelated Ricker lags also showed a strongly negative residual associated with the 1997 recruits and a strong positive residual associated with the 1990 recruits. Within the autocorrelated Ricker configurations, a 5-year recruitment lag using all males provided the best model with an AIC_c value of 118.0. Nevertheless, there is only weak evidence (i.e., $2 \leq AIC_c$ difference ≤ 4) that this model is

better than the autocorrelated Ricker models with 5- and 7- year lags using legal males (AIC_c values of 120.4 and 120.5, respectively).

For most configurations, the depensatory models had difficulty converging to realistic results. Constraining β to be nominally positive (i.e., $> 1.0 \times 10^{-7}$) improved model convergence, but model plots of residuals showed little improvement and AIC_c values indicated less parsimony compared to autocorrelated Ricker configurations. The only exception was a lag-5 autocorrelated depensatory model that readily converged and produced an AIC_c value of 119.1 (data not tabulated), suggesting no credible difference (i.e., AIC_c difference ≤ 2) from the lag-5 autocorrelated Ricker model (AIC_c value of 118.0; Table 2.3). However, the predicted values for the lag-5 autocorrelated depensatory model indicated overcompensation at spawner values much larger than observed abundances, and peak spawner abundance of 71.5 million males seemed unrealistic compared to either the standard or autocorrelated Ricker models. We concluded that depensation is not indicated in these S-R models for red king crab.

Given that only weak difference as the best model exists among autocorrelated Ricker models with lag-5 or lag-7 using legal males or lag-5 using all males, these autocorrelated models were re-examined using up to three α and/or β parameters. The optimal sequence of years varied with lag length and male currency. Configurations considering two periods were best represented with brood year periods of 1960–1974 and 1975–1999 for lag-5 models and periods of 1960–1972 and 1973–1997 for lag-7 models. Three periods

were best represented by brood year groupings of 1960–1974, 1975–1984, and 1985–1999 for lag-5 models and 1960–1972, 1973–1986, and 1987–1999 for lag-7 models. The smallest AIC_c value of 109.0 occurred for a lag-5 autocorrelated all-male Ricker with three α and one β parameters (Table 2.4; Figure 2.5). The second best model, with an AIC_c value of 113.3, was a lag-5 autocorrelated Ricker using legal males three α and one β parameters (Table 2.4). Under the criterion of Burnham and Anderson (2004), the all-male configuration substantially improved model fit, indicated by AIC_c value differences larger than 4, over alternative autocorrelated Ricker models with either single or multiple α and β parameters (Tables 2.4 and 2.5). We note that all models with three β parameters failed to converge without severely bounding the β parameters.

As a generalization, incorporation of multiple α parameters in model configurations resulted in greater productivity (larger estimated α) and, conversely, multiple β parameters resulted in reduced density-dependence (smaller β), during the early portion of the time series relative to a single α or β, respectively, for the entire time series. This is exemplified by a lag-5 autocorrelated Ricker based on all males and estimating three α and one β parameters (Figure 2.5a). In the configuration with a single α, peak recruitment of 3.4 million males corresponds with peak spawner abundance of 37.7 million males (Table 2.2). In contrast, the best model in which the time series is partitioned into three periods represented by different α parameters and a single beta parameter shows substantially different productivity among brood year groupings. Although peak recruitment for all periods occurs from 32.8 million spawning males (defined as $1/\beta$), the

Table 2.4. The AIC_c values from different configurations of an autocorrelated Ricker, lagged 5 and 7 years with legal males and 5 years with all males, model in which the time series is divided into up to three different segments, indicated by α and β quantities of one to three.

Lag-5 using legal males

	Number of α		
Number of β	one	two	three
one	120.4	119.0	113.3
two	117.5	119.8	116.3 [a]
three	119.8 [a]	122.4 [a]	118.4 [a]

Lag-7 using legal males

	Number of α		
Number of β	one	two	three
one	120.5	119.6	120.1
two	117.3	119.6	121.3
three	119.9 [a]	122.4 [a]	124.6 [a]

Lag-5 using all males

	Number of α		
Number of β	one	two	three
one	118.0	116.8	109.0
two	117.1	118.7	111.5 [a]
three	119.8 [a]	121.6 [a]	122.0 [a]

[a] Values for β were constrained to force model convergence.

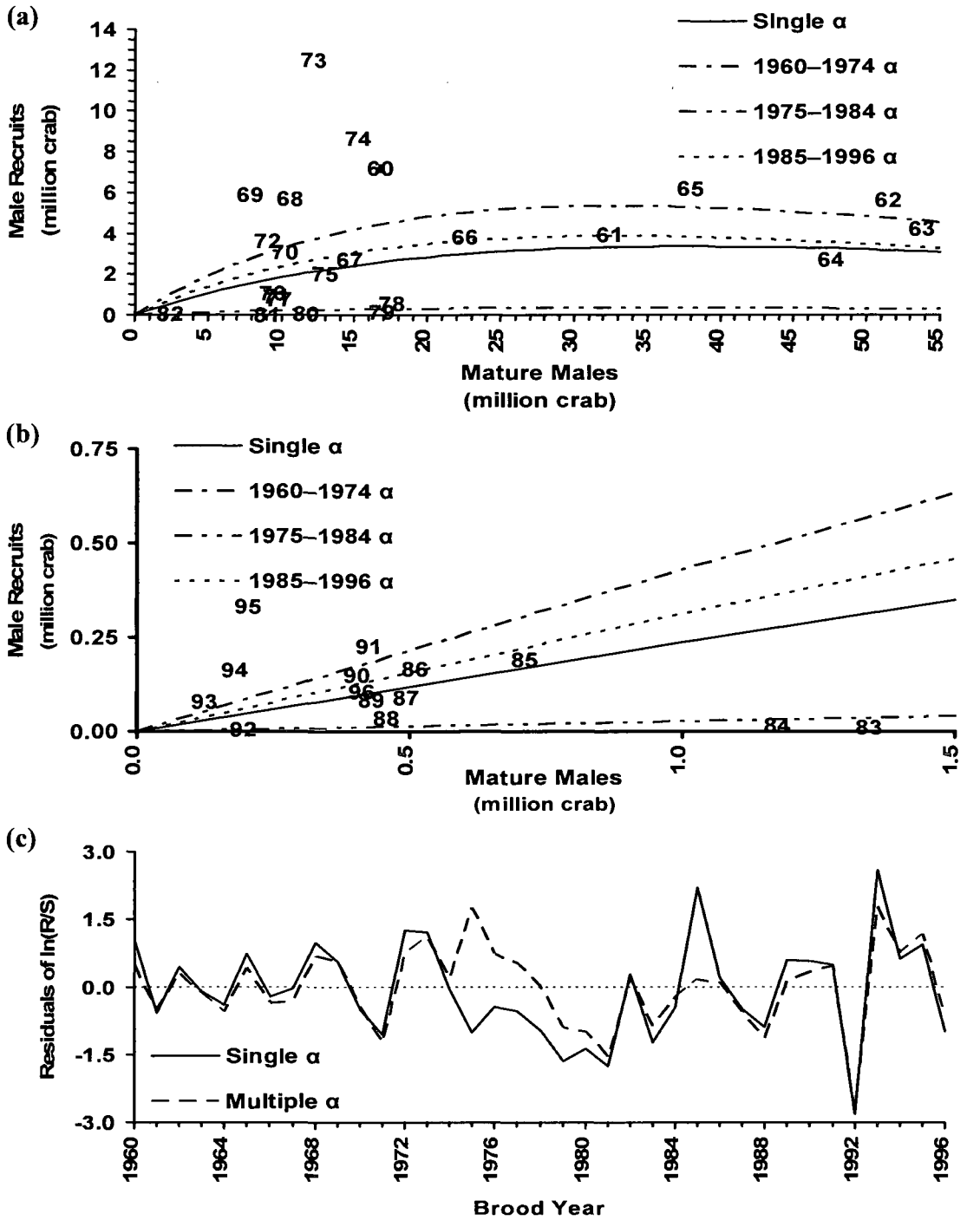


Figure 2.5. Lag-5 autocorrelated Ricker curves using all males and comparing a single α versus separate α parameters for the 1960–1974, 1975–1984, and 1985–1996 brood years and showing: (a) the entire time series; (b) the origins of curves; and (c) residuals patterns. Numerical labels in panels a and b are brood years.

Table 2.5. Parameter estimates and corresponding coefficients of variation (CV), residual sums of squares (RSS), and AIC_c values for selected lag-5 autocorrelated models with multiple α and β parameters. Multiple parameters for a model configuration are shown vertically with the corresponding brood years. Under "Crab," "A" indicates all males and "L" indicates legal males. Models consider 1960–1996 brood years for $n = 37$ observations.

Crab	Brood years	α	α CV	β	β CV	φ	φ CV	RSS	AIC_c
L	1960-1996	0.49	0.52	6.3×10^{-05}	0.53	0.75	0.10	45.62	120.4
L	1960-1974	1.36	0.53	3.2×10^{-05}	0.35	0.66	0.13	41.85	119.0
	1975-1996	0.22	0.42						
L	1960-1974	0.48	0.39	3.8×10^{-05}	0.81	0.66	0.14	40.11	117.5
	1975-1996			2.8×10^{-04}	0.24				
L	1960-1974	0.78	0.58	5.8×10^{-05}	0.61	0.63	0.15	39.58	119.8
	1975-1996	0.35	0.46	2.4×10^{-04}	0.31				
L	1960-1974	0.83	0.48	6.0×10^{-05}	0.49	0.51	0.22	33.16	113.3
	1975-1984	0.05	0.43						
	1985-1996	0.55	0.38						
A	1960-1996	0.24	0.48	2.7×10^{-05}	0.70	0.73	0.11	43.74	118.0
A	1960-1974	0.70	0.53	4.7×10^{-05}	0.39	0.64	0.14	39.37	116.8
	1975-1996	0.13	0.39						
A	1960-1974	0.25	0.36	1.7×10^{-05}	0.93	0.63	0.15	39.70	117.1
	1975-1996			1.4×10^{-04}	0.30				
A	1960-1974	0.51	0.56	3.6×10^{-05}	0.54	0.59	0.17	38.40	118.7
	1975-1996	0.17	0.41	1.1×10^{-04}	0.43				
A	1960-1974	0.44	0.46	3.1×10^{-05}	0.52	0.44	0.28	29.57	109.0
	1975-1984	0.03	0.39						
	1985-1996	0.32	0.34						

magnitude of recruitment varies among the three periods. For the first period, encompassing the 1960–1974 brood years, estimated peak recruitment is 5.3 million crab ($\alpha = 0.44$) and is noticeably higher (Figure 2.5b) compared to the single α model. Per-capita productivity during this first period is 1.4×10^{-5}. In the second period ($\alpha = 0.03$), the 1975–1984 brood years, the same level of peak male spawners results in a peak recruitment of only 0.4 million males and per-capita productivity is 8.9×10^{-7}. The final period, representing the 1985–1996 brood years ($\alpha = 0.32$), results in peak recruitment of 3.9 million males with per-capita productivity of 9.8×10^{-6}. Examination of residual patterns indicates improved model fit in the 1978–1996 brood years, but with only incremental improvement, at best, through the remainder of the time series (Figure 2.5c). Based on AIC_c value and the corresponding indication that S-R parameters changed over the time period, the optimal model becomes the lag-5 autocorrelated Ricker with three α's and a single β for the entire time series.

2.5 Discussion

Several studies have investigated S-R relationships for red king crab in Alaska (Reeves 1990; Greenberg et al. 1991; Zheng et al. 1995a, 1995b; Zheng and Kruse 2003), but few published analyses of S-R relationships exist for red king crab in the Gulf of Alaska. Schmidt et al. (1992) considered a variety of potential factors contributing to Kodiak red king crab stock recruitment, but concluded the time series of survey data was insufficient

to draw conclusions about the effect of adult females on subsequent age-5 male recruitment. Zheng et al. (1995a, 1995b) and Zheng and Kruse (2003) developed S-R relationships for red king crab in Bristol Bay, Alaska based on effective spawning biomass, determined as a function of mature females relative to functionally mature males. The Bristol Bay analyses (Zheng et al. 1995a, 1995b; Zheng and Kruse 2003) found an autocorrelated Ricker model provided a slightly better fit than a depensatory model because years of strong and weak recruitment occurred over separate periods (Zheng et al. 1995a).

Our Kodiak study similarly found autocorrelated models provided better fits than other models considered (Figures 2.3b, 2.3d, 2.3f, and 2.3h), with notable improvement during periods of negative residuals in the late 1970s to early 1980s and positive residuals in the 1990s (Figure 2.5c). Patterns near the origin further suggest autocorrelation with one series of brood years (the mid to late 1980s) with weak recruitment, followed by a second series of brood years (early 1990s) in which recruitment was still weak, but slightly better than the late 1980s (Figures 2.4a–d and 2.5b). Our optimal model, using all males in a lag-5 configuration with three α parameters to accommodate different productivity for brood years 1960–1974, 1975–1984, and 1985–1996, reduced overall autocorrelation across the time series to $\varphi = 0.44$ (Table 2.5), smaller than the 0.66 value found by Zheng et al. (1995a) for male red king crab in Bristol Bay. Although our use of male crab abundance as a proxy for spawning abundance may be less robust than using female data, a lack of female abundance data until 1972, well after years of high stock abundance and

strong recruitment, limits use of females in an S-R analysis for Kodiak red king crab. Nonetheless, autocorrelation is still suggested.

Among all autocorrelated Ricker configurations, estimated peak production of 2.0 to 3.4 million recruits resulted from 11.3 to 37.7 million male spawners. For our selected model with three α parameters, a total of 32.8 million male spawners provided an estimated 5.3, 0.4, and 3.8 million male recruits for the 1960–1974, 1975–1984, and 1985–1996 brood years, respectively. Because abundances of both spawners and recruits have been less than 1.0 million males since 1983, increased productivity for 1985–1997 relative to 1975–1985 seems contradictory with the failure of the population to rebuild following the commercial fishery closure since the early 1982. Data uncertainty could be a factor in this seeming inconsistency, and several strong outliers were evident in the residuals patterns from the S-R models. For example, the 1997 recruit estimate of 5 thousand male crab, accounting for ~25% of the residual sum of squares in the S-R models, is suspect and future analysis should explore the survey data from which this point is derived.

Another factor contributing to data uncertainty in the S-R relationship is the inability to accurately age red king crab, as well as assumed growth and maturity patterns (Powell 1967; McCaughran and Powell 1977; Bechtol and Kruse *in press*). Changing environmental conditions likely alter growth rates and maturity schedules. For example, periods of slow (1980–1984, 1992–1993), medium (1985–1991), and fast growth (1972–1979) were associated with molting probability shifts for red king crab in Bristol Bay

(Balsiger 1974; Zheng et al. 1995b). The Kodiak model assumption of a single S-R lag for the entire 45-year time series of likely introduces process error into the analysis. Incorporating variable growth and maturity rates for Kodiak red king crab, although more realistic, would have introduced complexity and uncertainty into the S-R analysis because of the lack of annual data. To maintain a relatively simple S-R model, we assumed long-term population patterns to be represented by a single time lag between the year of parental stock reproduction and the year of recruitment. Based on the growth analysis of McCaughran and Powell (1977), our sensitivity analysis considered time lags ranging from 5 to 8 years between reproduction and recruitment. The optimal model is a lag-5 autocorrelated Ricker based on all-males and using three α and one β parameter to accommodate different productivity periods (Tables 2.3 and 2.4). Ultimately, a 5-year mean lag between reproduction and model recruitment implies a 6-year lag to legal size, shorter than the 7–8 years estimated by McCaughran and Powell (1977), and perhaps suggesting a compensatory demographic mechanism of faster growth for what has become a depressed population.

The inconsistency between productivity and abundance may also indicate depensation in the Kodiak population. For example, crab abundance may be regulated at a low-density, stable equilibrium by predation, or a "predator pit" (May 1977; Peterman 1977; Liermann and Hilborn 2001). Yet, our analysis through a depensatory model, even when substituting depensation for only one or two of the periods in our optimal model, failed to confirm depensation. Liermann and Hilborn (2001) concluded that, because demography

and environmental variability make depensation very difficult to detect, a lack of evidence cannot be interpreted as evidence that depensation is rare or unimportant. In depensatory cases, future increases in the population may occur only under unusually favorable environmental conditions, or declines in predation that result in increased recruitment.

Analysis of stock productivity should have sufficient contrast between years of high and low abundances to represent the range of potential productivity for a population (Hilborn and Walters 1992), but our analysis of S-R relationships for Kodiak red king crab was constrained in this regard by three issues. First, despite the availability of 45 years of abundance and recruitment data, values of stock abundance and recruitment for a large portion of the assessed years, those since the 1980s, were at low levels near the S-R curve origin (Figures 2.4a–d, and 2.5b). These points near the origin represented over half of the data, but introduced little contrast into the S-R relationship. Second, years of highest recruitment occurred in the early 1960s, corresponding to brood years in the late 1950s for which abundance estimates of the reproductive stock are unavailable (Table 2.2). Although previous research suggested that recruitment in the early 1960s was anomalously high (Rothschild et al. 1970; Burgner 1972; Bechtol and Kruse *in press*), the strong recruitment levels observed from moderate spawning populations during that period, if under optimal environmental conditions, would fit well with the S-R relationships from our study. Third, the Kodiak stock was subject to high male harvest rates on a decreasing population abundance in the late 1970s, coupled with sex ratios

increasingly skewed toward females (Orensanz et al. 1998; Bechtol and Kruse *in press*). The resulting localized recruitment overfishing, coupled to recruitment failures in the mid 1980s, essentially created a "one-way trip," limiting data utility for stock dynamics modeling (Hilborn and Walters 1992).

In addition to the contradiction between relatively high productivity and low observed abundance, there other indications of reduced resiliency in the population. Bechtol and Kruse (*in press*) noted increased variability in natural mortality following the regime shift in the mid 1970s. The magnitude of annual fluctuations in natural mortality again increased dramatically after 1988, complemented by a general increase in mean annual mortality. Such a pattern may indicate reduced resiliency due to low population size and a truncated age structure (Leaman and Beamish 1984; Kruse 1993; Berkeley et al. 2004). Kruse (1993) concluded that skip-molt males (those not molting in the current year) may predominate in mating success. Because males skip-molt at increasing frequency with growth beyond 125 mm CL (McCaughran and Powell 1977), our size of model recruitment, and larger males tend to have greater reproductive success (Paul and Paul 1997), reproductive contribution and skip-molting are both anticipated to increase with crab size. However, our lag-5 autocorrelated models showed slight improvement in AIC_c values if using an all male versus legal male currency with a single α and strong improvement with three α's (Table 2.4). Reproductive contribution by sublegal males arguably varies annually in response to environmental conditions that promote or suppress strong survival and/or faster growth, and also large male availability, which

depends on management strategies and corresponding fishing mortality. Our analysis, while characterizing long-term population trends using a single male currency, suggests sublegal males have made important reproductive contributions to the Kodiak stock, perhaps at the expense of population resiliency. Finally, the reduction in red king crab abundance around Kodiak was accompanied by a severe range contraction. Dramatic geographic reductions from the 1970s to the 1980s were documented by the pot survey, which was conducted until 1986 (Johnson 1990). Fine-scale patterns in the red king crab spatial distribution cannot be derived from the more recent (1986–present) trawl survey data because of systematic survey bias, but verbal reports from local vessel operators continue to indicate a very limited spatial crab distribution. Thus, crabs are recruiting into a much smaller habitat area likely subject to intense competition and/or predation, including cannibalism. Although low population size and high interannual survey variability have substantially increased measurement error in the stock assessment (Bechtol and Kruse *in press*), we postulate that low population abundances in recent years makes the population particularly vulnerable to density-dependent factors, such as difficulty in finding mates during the mating season. These aspects reiterate the need to maintain a broad age-structure to provide resiliency in managed populations of long-lived species (Leaman and Beamish 1984; Kruse 1993; Berkley et al. 2004).

Our optimal model indicated at least three periods of different productivity (Table 2.5); estimated transitions in 1975 and 1985 would have been expressed as recruitment in 1980 and 1990 by the lag-5 model. We did not conduct an exhaustive search of potential

regime transition points, and future analysis should consider time-varying parameters through procedures such as a Kalman filter (Peterman et al. 2000). However, our transitions are consistent with the generally recognized climate regime shifts of 1976 and 1989 for the North Pacific (Anderson and Piatt 1999; Hare and Mantua Hare 2000; Kruse 2007; Mueter et al. 2007), particularly given that response to ecological changes can vary temporally by species (Rodinov and Overland 2005). In particular, the climate regime shift in the North Pacific during the late 1970s was associated with aspects such as increased ocean temperatures and increased abundances of predatory fishes, such as Pacific cod *Gadus macrocephalus*. A study of the decline in the Kachemak Bay stock of northern shrimp *Pandalus borealis* found that a strong increasing trend in natural mortality followed the 1976–1977 regime shift, paralleling trends in increased Pacific cod abundance (Fu and Quinn 2000; Fu et al. 2000). That study found natural mortality to be the most important factor controlling this stock during the late 1970s and early 1990s. Red king crab instars are susceptible to predation by a variety of groundfish and shellfish (e.g., Jewett 1978; Jewett and Powell 1979), including cannibalism (Broderson et al. 1990). We speculate that predation is a likely cause for increased natural mortality and reduced recruitment during the latter portion of the time series examined here. A cursory analysis of the ADF&G pot survey data revealed a strong increase in relative abundance of Pacific cod in nearshore waters around Kodiak at a time when the king crab population drastically declined (results not shown). But, predation on any life stage of red king crab, and the corresponding impact on future recruitment, has been poorly documented (Livingston 1989; Dew and McConnaughey 2005; Zheng and Kruse 2006).

Our study represents the first development of an S-R relationship for the red king crab population around Kodiak, Alaska. A density-dependent relationship is suggested by a dome-shaped relationship in the S-R data. Future analyses of Kodiak red king crab should examine temporal changes in stock and recruitment with respect to oceanographic conditions and ecological factors. In addition, the potential interaction between crab stocks and other fisheries, such as bottom trawl fisheries for groundfish and shrimp, merits further research because of potential impacts to the benthic crab habitats and direct, but often undocumented, crab mortality, particularly egg-bearing females (Armstrong et al. 1993; Dew and McConnaughey 2005). Moreover, the relationship between crab recruitment and environmental and ecological factors, such as temperature effects on match-mismatch of crab larvae and their prey, is of particular interest, especially given that larvae must feed within 2–6 days of hatching for optimal survival (Paul et al. 1989). We will explore these relationships more completely in a forthcoming paper.

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Chapter 3: Factors Affecting Red King Crab Recruitment around Kodiak Island, Alaska[3]

3.1 Abstract

Waters around Kodiak Island in the Gulf of Alaska once supported the world's largest fishery for red king crab *Paralithodes camtschaticus*. Commercial fisheries occurred at low levels beginning in 1937, but increased rapidly in the 1960s to a peak harvest of 42,800 mt in 1965. Stock abundance declined in the late 1960s, moderated in the 1970s, and collapsed in the early 1980s, but a commercial fishery closure since 1983 has not resulted in stock recovery. We used a modified autocorrelated Ricker spawner-recruit model to examine crab recruitment patterns for the 1964–1999 brood years (n = 36 observations) in relationship to biotic and abiotic variables hypothesized to be important to the survival of early life stages of Kodiak red king crab. Our hierarchical approach for model selection used AIC_c, the Akaike Information Criterion corrected for small sample size. Results revealed a strong negative association between biomass of age 3+ Pacific cod *Gadus macrocephalus* and crab recruitment. The Kodiak stock of red king crab declined following a period of high harvest rates in the late 1960s that skewed sex ratios and compromised reproductive potential. Then in the late 1970s, it appears that predation on crab may have increased, possibly due increased Pacific cod biomass combined with a

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[3] Bechtol, W.R., and G.H. Kruse. In preparation. Factors affecting red king crab recruitment around Kodiak Island, Alaska. Prepared for submission to: "Biology and management of exploited crab populations under climate change," University of Alaska Sea Grant.

nearshore shift in cod spatial distribution that resulted from warmer temperatures associated with a climate regime shift. Inclusion of percent cloud cover at Kodiak, Alaska, as a second ecological variable slightly improved model fit, but the associated mechanism is unclear.

3.2 Introduction

The Kodiak Island area in the northern Gulf of Alaska (Figure 3.1) once supported the world's largest fishery for red king crab *Paralithodes camtschaticus*. Commercial harvests from this area first occurred in the 1930s, with exploratory harvests continuing into the late 1950s. These historical crab harvests largely occurred in winter by a small number of purse seine vessels (< 18-m length overall) that harvested salmon in summer (Gray et al. 1965; Spalinger 1992). However, small vessel size and lack of live tanks limited the fishery to low-level harvests in inshore, shallow waters close to landing facilities. With the introduction of vessels designed for crab fishing, annual landings increased rapidly in the 1960s to a peak harvest of 42,800 mt (94.4 million lb) in 1965, but harvest levels declined, and the commercial fishery fluctuated at low levels before being closed in 1983 (Spalinger and Jackson 1994; Bechtol and Kruse *in press* a). Several management measures, such as time and area closures and adjusted minimum size limits, failed to curtail the decline (Gray et al. 1965; Spalinger 1992). A commercial fishery closure since 1983 has not resulted in recovery of this severely depleted stock.

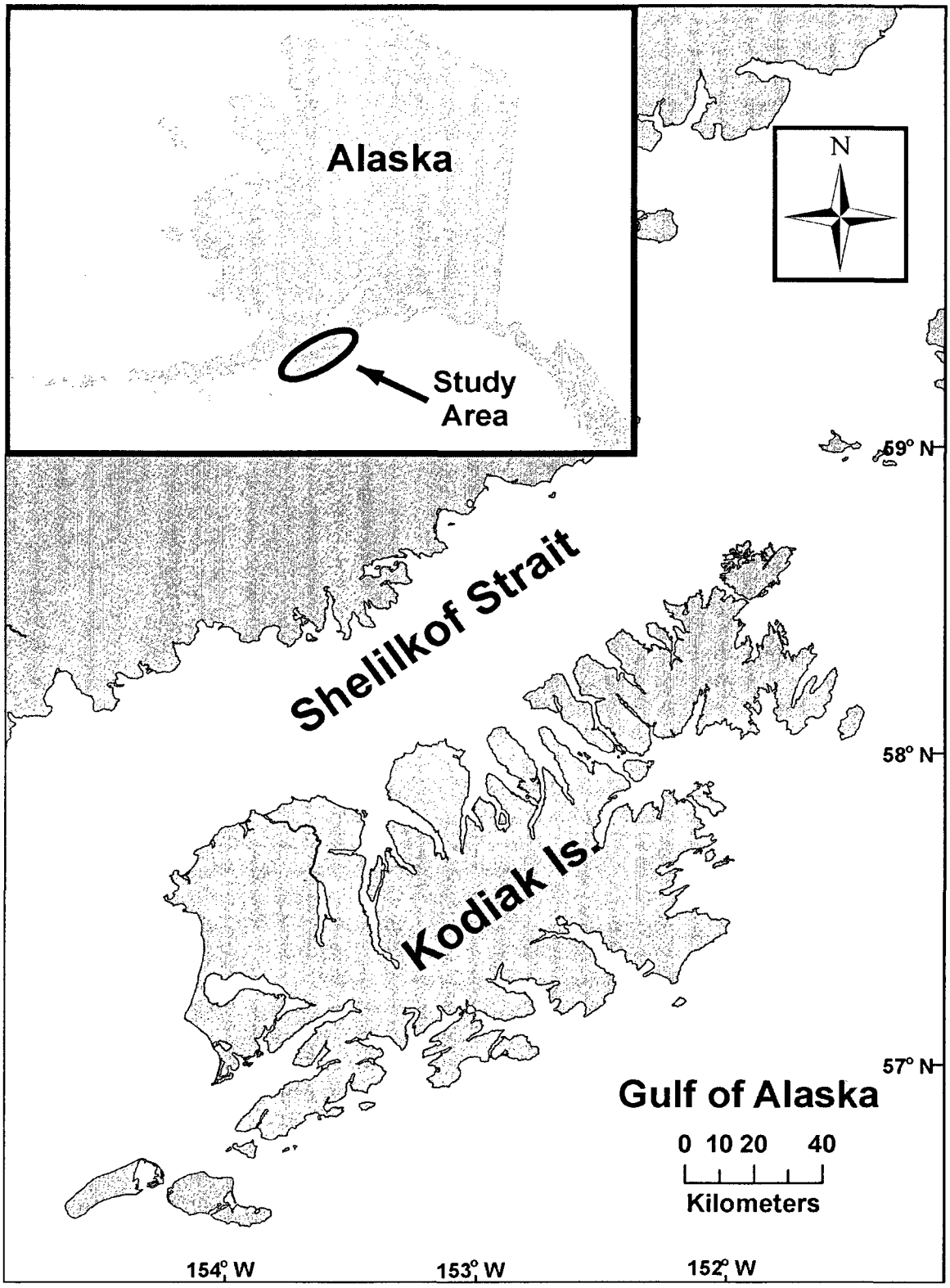

Figure 3.1. Location of the Kodiak study area in the northern Gulf of Alaska.

Our study goal was to determine conditions that may have contributed to the rise, fall, and continued depressed status of the red king crab stock around Kodiak Island through numerical modeling in a retrospective analysis. Previous analyses of Alaskan crab population dynamics focused on Bering Sea stocks, mainly red king crab and Tanner crab *Chionoecetes bairdi* in Bristol Bay and snow crab *Chionoecetes opilio* in the eastern Bering Sea (Zheng and Kruse 2000). Zheng and Kruse (2003) used a length-based analysis of trawl survey time series to investigate stock-recruit relationships for these three stocks. For both Tanner crab and snow crab, cyclic patterns in the stock-recruit observations were thought to be associated with environmental forcing. For red king crab, stock-recruit relationships suggested density-dependent effects, although recruitment trends were also consistent with decadal climate shifts, so results were equivocal. In an analysis of recruitment patterns, seven of 15 crab stocks in the Gulf of Alaska and Bering Sea had trends consistent with decadal climate shifts, with periods of strong Aleutian lows coinciding with weak recruitment (Zheng and Kruse 2000). Red king crab in Bristol Bay and the Gulf of Alaska generally shared this decadal pattern.

In previous analyses, we: (1) reconstructed stock and recruitment abundances in Kodiak red king crab during 1960 to 2004 (Figure 3.2; Bechtol and Kruse *in press* a); and (2) examined potential stock-recruit relationships (Bechtol and Kruse *in press* b). Although changes in abiotic and biotic factors may influence stock productivity at any red king crab life stage, these effects likely are most pronounced during early life history, particularly larval and early benthic stages. Here, we explored evidence of relationships

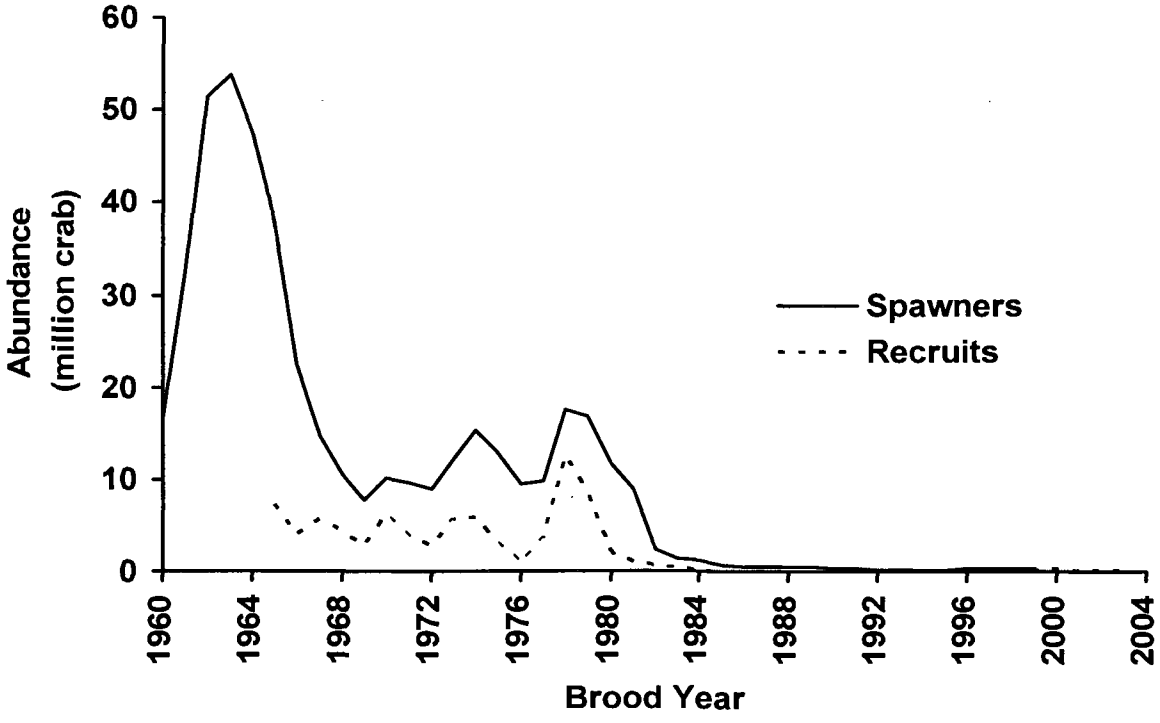

Figure 3.2. Annual estimated abundances of male spawners and lag-5 recruits for Kodiak red king crab, 1960-2004.

between crab recruitment around the Kodiak Island archipelago and environmental and ecological factors. The application of models that combine population dynamics (stock-recruit) and ecological factors (e.g., predator-prey, fishery oceanography) allowed us to better assess conditions that contributed to the increase and subsequent collapse of the Kodiak king crab stock, as well as potential impediments to rebuilding (e.g., low spawning stock vs. predation vs. oceanographic conditions) that should be considered in ongoing restoration efforts.

3.3 Crab Biology and Ecological Effects Relevant to Recruitment

Red king crab recruitment is believed to depend primarily on survival during early life history (Zheng and Kruse 2000). A summary of ecological factors affecting early life history in red king crab follows with a more detailed review provided in Appendix 1. Adult females mate annually during March and April with the eggs then incubated on the female's abdomen for approximately 300 d. Embryos hatch into pelagic larvae from March to May, inhabiting the water column at depths < 100 m. Larvae molt through four zoeal stages, lasting approximately two weeks each. Early instar zoea must feed within 2-6 d to survive, tending to be phytoplanktivorous with a preference for the diatom *Thalassiosira* sp. (Paul et al. 1989; Shirley and Shirley 1989). Conditions promoting a phytoplankton community dominated by *Thalassiosira* sp., and, thus, zoea survival, include a stable, stratified water column and relatively cool sea surface temperatures

(Ziemann et al. 1990; Bienfang and Ziemann 1995). Spring phytoplankton production also depends on incident light, so more extensive cloud cover could delay and reduce the spring bloom (Bienfang and Ziemann 1995; Tyler and Kruse 1995; Cooney 2007); increased cloud cover also reduces surface water warming (Weingartner 2007). Surviving zoea metamorphose into a glaucothoe stage that uses a well-developed swimming ability to search for preferred habitat of nearshore, rocky substrate with high-profile sessile fauna (Powell and Nickerson 1965; Armstrong et al. 1993; Stevens and Kittaka 1998; Loher 2001). The glaucothoe then molt into a benthic, largely solitary, existence as the first red king crab instars during May to July around Kodiak. At 1 to 2 years after settlement, the juvenile king crab begin to form pods and move to deeper water. Due to their small size, all juvenile king crab are susceptible to predation by a wide variety of shellfish and groundfish, including cannibalism (Broderson et al. 1990). However, predation risk increases for all life stages during the soft-shell period following molting. Red king crab undergo 7 to 8 molts the first year after settlement, decreasing to 1 to 2 molts in the fourth year (McCaughran and Powell 1977).

3.4 Methods

Estimates of spawners and recruits derive from a stage-based stock reconstruction of male and female red king crab using pot and trawl surveys from 1972 to 2004 and commercial harvests of male crab from 1960 to 1982 (Bechtol and Kruse *in press* a).

Male red king crab recruited into the model at 125 to 144 mm CL, assumed to be one molt prior to legal size. Based on a growth analysis of Kodiak red king crab by McCaughran and Powell (1977), we assumed this pre-legal size is achieved 5 to 8 years after egg fertilization. A subsequent study (Bechtol and Kruse *in press* b) of potential stock-recruit relationships determined that the most parsimonious model was a lag-5 autocorrelated Ricker in which the time series was broken into three periods representing brood years for 1960–1974, 1975–1984, and 1985–1996. We applied the same three productivity periods in this study.

Following Tyler and Kruse (1996a, 1996b), we explored an events-time modeling procedure that considers hypotheses about ecological factors operating during key life history stages. We specifically examined factors considered to be important to the larval to settlement stages, and to the juvenile benthic to recruitment stages. During the larval to settlement stages, the most critical factors are anticipated to be those affecting stratification and temperature of shallow, subsurface waters from March through June each year. It is acknowledged that, in general, these factors do not directly kill crab larvae, such as might occur through mechanical damage, but instead are indices of conditions that promote or impede larval survival. We hypothesize that predation is the predominant factor controlling survival after glaucothoe settlement, although predation by planktivorous fish during the pelagic larval stage is also plausible. In addition, non-directed fishing activities (i.e., those not directed at red king crab) potentially affect survival of post-settlement crab stages through both habitat damage and direct mortality

(Armstrong et al. 1993). We assembled 14 ecological datasets on variables for which associations with king crab recruitment were postulated (Table 3.1). The first nine datasets, representing factors potentially affecting stratification and temperature of marine surface and shallow, subsurface waters in the vicinity of Kodiak Island during the pelagic larval stage lasting from March through June, included:

(1) sea level pressure at Kodiak, Alaska as an index inversely related to storm activity and water column stratification;

(2) wind speed cubed as an index of surface wind energy and inversely related to water column stability;

(3) Pacific Decadal Oscillation as an index related to water column stability;

(4) freshwater discharge data for the Copper River and other Gulf of Alaska systems as an index of ACC flow and freshwater-driven water column stratification;

(5) percent cloud cover at Kodiak, Alaska as an index inversely related to incident light and surface water warming;

(6) sea surface temperature in the area 55 to 60 degrees N and 148 to 158 degrees W as an index of shallow subsurface conditions off Kodiak;

(7) seawater temperature collected from the surface to 250 m at the GAK1 station off Seward, Alaska as an index of surface and subsurface conditions in the ACC upstream of Kodiak;

(8) salinity collected from the surface to 250 m at the GAK1 station off Seward, Alaska as an index of water column stratification in the ACC upstream of Kodiak; and

Table 3.1. Ecological parameters examined for relationships to stock-recruit residuals.

Data Series [a]	Abbreviation	Years considered	Data source
Kodiak sea level pressure	SLP	1960–2004	http://www4.ncdc.noaa.gov/cgi-win/wwcgi.dll?wwDI~StnSrch~StnID~20021863
Kodiak wind speed cubed	WS3	1960–2004	http://www4.ncdc.noaa.gov/cgi-win/wwcgi.dll?wwDI~StnSrch~StnID~20021863
Pacific Decadal Oscillation	PDO	1960–2004	http://www.cgd.ucar.edu/cas/catalog/climind/soi.html
Gulf of Alaska freshwater discharge	DCG	1960–2004	Royer and Grosch (2007)
Kodiak cloud cover	CLD	1960–2004	http://www4.ncdc.noaa.gov/cgi-win/wwcgi.dll?wwDI~StnSrch~StnID~20021863
Kodiak sea surface temperature	SST	1960–2004	http://nomads.ncdc.noaa.gov/#climatencdc
GAK 1 water temperature	GAT	1970–2004	http://www.ims.uaf.edu/gak1
GAK 1 salinity	GAS	1970–2004	http://www.ims.uaf.edu/gak1
Trident Basin water temperature	TRI	1970–2004	C. Worton, Alaska Department of Fish and Game (pers. comm.)
Walleye pollock age 3+ female spawning biomass	POL	1961–2004	M. Dorn, National Marine Fisheries Service (pers. comm.)
Pacific halibut age 10+ biomass	HAL	1960–2004	S. Hare, International Pacific Halibut Commission (pers. comm.)
Pacific cod age 3+ biomass	COD	1964–2004	Thompson and Dorn (2005)
Arrowtooth flounder age 3+ biomass	ATF	1961–2004	Turnock et al. (2005)
Kodiak trawl shrimp	SHR	1960–2004	G. Smith, Alaska Department of Fish and Game (pers. comm.)

[a] See text for details.

(9) seawater temperature at 10 m depth (MLLW) in Trident Basin near the community of Kodiak as an index of shallow subsurface conditions around Kodiak.

For each dataset, data recorded either daily or monthly were averaged across March to June to obtain an annual estimate for the pelagic larval time period.

Although a wide variety of potential crab predators exists, there are few predators for which a long time series of data is available. The next four datasets were treated as annual indices of potential predator populations in the Gulf of Alaska and included (Table 3.1):

(10) walleye pollock *Theragra chalcogramma* during 1961–2004 in the Gulf of Alaska;

(11) age 10+ abundance of Pacific halibut *Hippoglossus stenolepis* in International Pacific Halibut Commission Management (IPHC) Area 3A;

(12) age 3+ biomass of Pacific cod *Gadus macrocephalus* during 1961–2004 in the Gulf of Alaska; and

(13) age 3+ biomass of arrowtooth flounder *Atheresthes stomias* during 1964–2004 in the Gulf of Alaska.

The survey biomass estimates are derived from IPHC trawl and longline surveys, NMFS groundfish surveys, and NMFS triennial surveys (Table 3.1). Of these fish populations, walleye pollock tends to be planktivorous and was hypothesized to feed on pelagic larval stages of red king crab, whereas Pacific halibut, Pacific cod, and arrowtooth flounder were hypothesized to prey on benthic life stages of red king crab.

The final dataset, treated as an index of the potential impacts of a benthic trawl fishery on benthic habitat and undocumented direct crab mortality, was:

(14) annual catch biomass of the benthic trawl fishery for shrimp during 1960–1985. This trawl fishery has either been closed or attracted no harvesting effort since the mid 1980s due to low shrimp stock abundance (Jackson and Ruccio 2003). The extent of spatial overlap between juvenile red king crab and trawl fishing effort likely exhibits a high degree of fine scale variability and is difficult to ascertain from the available data. However, it was assumed that greater trawl fishery removals during the active fishery resulted in greater impacts to crab and to crab habitat.

Standardized anomalies were developed for each set of annualized data by subtracting the grand mean from each year's observation, then dividing by the standard deviation. To examine potential relationships between crab recruitment and ecological variables, we first plotted the anomalies against the residuals of the optimal lag-5 autocorrelated Ricker model from Bechtol and Kruse (*in press* b). Second, we incorporated ecological factors into the Ricker equation:

$$\begin{aligned} R_t &= \alpha S_{t-k} e^{-\beta S_{t-k} + \nu_t + \theta_t} \\ \theta_t &= \gamma_{1_1} X_{1,t-k+j_1} + \Lambda + \gamma_p X_{p,t-k+j_p} \quad , \end{aligned} \tag{3.1}$$

where α is a parameter representing per-capita productivity at low stock size, β is a parameter controlling the degree of density dependence, R is recruit abundance in year t,

S is stock size lagged k years from year t, $X_1 \ldots X_p$ are the time series of ecological anomalies with corresponding coefficients $\gamma_1 \ldots \gamma_p$, and $\{v_t\}$ is the set of random variables that account for unexplained variation (Ricker 1954, Quinn and Niebauer 1995; Pyper and Peterman 1998; Quinn and Deriso 1999). The ecological anomalies are offset from the brood year by $j_1 \ldots j_p$ years, ultimately representing the year(s) after reproduction in which an anomaly affects the crab; e.g., an offset of 0 corresponds to the first year of crab life. To reduce the likelihood of spurious correlations, we limited the offsets for the first nine factors and for pollock, those factors believed to primarily affect the pelagic larvae stage (Table 3.1), to 0; the offsets for the remaining predators and for the shrimp fishery were limited to a range of 1–5 years. We assumed the v_t to be autocorrelated, as given by $v_t = \delta_t + \varphi v_{t-1}$, where δ_t is environmental white noise, assumed to be distributed as $N(0,\sigma^2)$, Equation 3.1 incorporates autocorrelation effects with φ representing the degree of autocorrelation among residuals. Because preliminary results suggested that the inclusion of specific ecological datasets effectively eliminated the significance of the autocorrelation parameter, φ, as an explanatory variable, we also fitted the data to a Ricker model without autocorrelation by setting $\varphi = 0$. Note that setting $\varphi = \gamma_i = 0$ results in a standard Ricker model. We examined a k lag of five years, the lag providing the best S-R fits (Bechtol and Kruse *in press* b). This equation was linearized by taking logarithms:

$$\ln\left(\frac{R_t}{S_{t-k}}\right) = \ln(\alpha) - \beta S_{t-k} + v_t + \theta_t \ . \qquad (3.2)$$

Peak recruitment in the Ricker model occurs at a stock size (S_p) of $1/\beta$. Per-capita productivity was allowed to vary among three critical time periods representing brood years 1964–1974, 1975–1985, and 1985–1999. To provide comparable results among datasets of different lengths, only the 1964 to 1999 brood years were examined, giving $n = 36$ observations for reproduction to recruitment lags of 5 years.

In addition to examining residual patterns, model selection involved comparing AIC_c values (Burnham and Anderson 2004):

$$\begin{aligned} \hat{\sigma} &= \sqrt{\frac{RSS}{n-p}} \\ -2\ln L &= n\ln\left(2\pi\hat{\sigma}^2\right)+\frac{RSS}{\hat{\sigma}^2} \\ AIC_c &= -2\ln L + 2p + \frac{2p(p+1)}{n-p-1} \end{aligned} \tag{3.3}$$

where n is the number of observations, RSS is the residual sums of squares, p is the number of parameters in the model, and AIC_c is a formulation of the Akaike Information Criterion corrected to accommodate small sample sizes. According to Burnham and Anderson (2004), no credible evidence exists to eliminate competing models with AIC_c differences ≤ 2, weak evidence exists for elimination with differences of 2 to 4, and definite evidence exists for differences ≥ 4. Our base model was the lag-5 autocorrelated

Ricker model previously shown to be the most parsimonious model (Bechtol and Kruse *in press* b).

We employed an hierarchical approach in which models were first examined with a single ecological parameter at lags as described above ranging from 0 to 5 years, representing the crab age in years at which the ecological variable has the strongest effect. If a single ecological factor was found to improve model fit based on AIC_c values, a second ecological parameter was incorporated in conjunction with the first. This process was repeated until no credible model improvement occurred. To simplify reporting of results, a given ecological dataset and lag is signified by the Table 3.1 data abbreviation combined with the effect lag, e.g., HAL-1 is halibut with a lag-1 year effect. Models were implemented in AD Model Builder (Otter Research Ltd., Sidney, B.C., Canada), with additional validation using Microsoft Excel (Microsoft Corporation, Redmond, Washington). Relative precision of an estimated parameter was reported as the coefficient of variation *(CV)*, the standard error divided by the estimate. Standard errors were obtained as an estimate in the output from AD Model Builder, except that a bootstrap approach (Efron and Tibshirani 1993) was used for models lacking autocorrelation. For the bootstrap, model residuals are resampled with replacement and added to the predicted values, and the model re-run to obtain new parameter estimates. This process was replicated 1,000 times for each model, with the standard deviations of the bootstrap parameters serving as estimates of the standard errors of the parameter estimates.

After determining our preferred model(s), we examined the effects of the ecological factors on potential stock production and harvest removals. By assuming the derived parameters represents the population in equilibrium, the maximum sustained catch (MSC) can be calculated as the maximum difference between recruitment (R_m) and the spawner abundance (S_m) needed to maintain the level of production (Quinn and Deriso 1999), such that MSC = R_m S_m. For the Ricker curve, MSC occurs

$$\begin{aligned} &\alpha'(1-\beta S_m)e^{-\beta S_m} = 1 \\ &\alpha' = \alpha e^{\gamma X} \quad , \end{aligned} \tag{3.4}$$

where α, β, γ, and X are as in Equation 3.1. To represent the current status of the stock, α and β were set equal to parameter estimates for brood years 1985–1999 from the preferred model. Finally, the harvest rate at MSC was calculated as μ_m = MSC/R_m. Given the high variability in the environmental factors, we estimated MSC at three different levels of the environmental variable, representing the first three quartiles of the distribution of the environmental anomaly.

3.5 Results

Graphical analysis of ecological parameters against the crab S-R residuals revealed few strong relationships (results not shown). Although strong serial patterns were evident in the plots of anomalies against S-R residuals, there were also indications of rapid and drastic changes in relationships. We made particular note of a negative S-R residual associated with recruits in 1997, a data point that has previously drawn suspicion (Bechtol and Kruse *in press* b). However, positive S-R residuals prior to the 1980s tended to be associated with negative ecological anomalies, with generally negative S-R residuals associated with positive ecological anomalies in other years.

Our model provided nonsensical results (e.g., $\beta < 0$ or unrealistically high S_p) when run with the GAK1 salinity and temperature, Trident Basin temperature, and shrimp harvest datasets, likely due to inconsistent overlaps with crab recruitment time series; these data were eliminated from further consideration.

Among models with a single ecological parameter, the smallest AIC_c value was obtained with a Ricker curve lacking autocorrelation and lag-2 Pacific cod anomalies (COD-2; AICc value of 96.9; Table 3.2). A strongly negative effect (γ = -1.56; CV = 0.22) between Pacific cod and age-2 crab was indicated (Table 3.3). With an AIC_c difference of 9.9, this model clearly outperformed the base model (AIC_c = 106.8). However, there is little credible evidence that the COD-2 model differed from the autocorrelated COD-2

Table 3.2. Comparison of AIC_c values for selected lag-5 Ricker models with and without autocorrelation and incorporating (A) one, (B) two, and (C) three ecological parameters (defined in Table 3.1), with ecological effects lagged from 0 to 5 years. Models consider 1964-1999 brood years (n = 36 observations), with "F" indicating a fixed parameter to create a fuller model.

Parameter	Models without autocorrelation						Models with autocorrelation					
	Lag (years)						Lag (years)					
	0	1	2	3	4	5	0	1	2	3	4	5
A. One ecological parameter models												
SLP	114.6	114.6					109.7	109.8				
WS3	114.1	109.6					108.5	105.8				
PDO	111.0	114.6					107.0	109.6				
DCG	111.5	114.2					107.7	108.1				
CLD	113.6	114.2					104.3	109.7				
SST	111.8	114.5					107.1	109.7				
POL	101.4	108.7					102.2	106.2				
HAL		112.7	111.8	111.6	111.2	110.3		108.2	107.7	107.9	107.6	106.6
COD		100.5	96.9	98.3	99.2	100.4		102.5	98.9	100.5	101.0	102.2
ATF		110.1	111.4	112.6	113.3	113.8		106.8	107.2	107.9	108.2	108.4
B. Two ecological parameter models												
SLP	100.0	99.9					102.4	102.4				
WS3	95.0	99.7					98.1	101.9				
PDO	99.7	98.8					102.1	101.5				
DCG	97.2	99.3					99.9	101.6				
CLD	94.5	100.0					95.6	102.5				
SST	99.9	99.5					102.2	102.0				
POL	99.0	99.1					102.3	101.8				
HAL		99.5	99.6	99.9	100.0	100.0		101.8	102.3	102.4	102.4	102.4
COD		99.9	F	99.9	99.8	99.7		102.4	F	102.4	102.3	102.4
ATF		100.0	100.0	99.9	99.9	99.8		102.5	102.5	102.5	102.4	102.3

Table 3.2 (continued)

Parameter	Models without autocorrelation						Models with autocorrelation					
	Lag (years)						Lag (years)					
	0	1	2	3	4	5	0	1	2	3	4	5
B. Two ecological parameter models (continued)												
SLP	101.3	101.3					103.9	104.0				
WS3	97.9	101.0					101.1	103.4				
PDO	100.8	100.2					103.4	103.0				
DCG	99.0	101.0					101.9	103.4				
CLD	96.0	101.3					97.8	104.0				
SST	101.1	101.0					103.5	103.6				
POL	100.0	100.9					102.4	103.5				
HAL		100.1	100.3	100.7	100.9	101.1		103.0	103.2	103.5	103.7	103.8
COD		101.0	99.9	F	101.2	101.2		103.6	102.4	F	103.8	103.9
ATF		101.3	101.4	101.4	101.3	101.3		104.0	104.0	104.0	104.0	104.0
C. Three ecological parameter models												
SLP	95.9	97.6					97.6	99.2				
WS3	94.6	97.5					96.8	98.5				
PDO	97.0	95.8					98.2	97.7				
DCG	92.6	96.6					93.8	97.3				
CLD	F	97.8					F	99.0				
SST	97.8	97.2					99.2	98.8				
POL	96.7	96.7					98.1	98.5				
HAL		97.8	97.8	97.8	97.7	97.6			99.2	99.2	99.0	99.1
COD		97.7	F	97.6	97.3	96.8			F	99.1	99.0	98.6
ATF		97.8	97.8	97.8	97.8	97.8			99.2	99.2	99.2	99.2

Table 3.2. (continued)

Parameter	Models without autocorrelation					
	Lag (years)					
	0	1	2	3	4	5
C. Three ecological parameter models (continued)						
SLP	98.0	98.2				
WS3	F	96.5				
PDO	98.3	96.0				
DCG	96.3	96.6				
CLD	94.6	98.2				
SST	98.2	95.7				
POL	95.9	97.4				
HAL		98.3	98.4	98.3	98.1	98.0
COD		98.2	F	98.4	98.2	97.4
ATF		98.3	98.4	98.3	98.2	98.2
SLP	98.2	99.2				
WS3	97.5	99.0				
PDO	98.2	97.4				
DCG	94.9	98.6				
CLD	F	99.3				
SST	99.4	98.8				
POL	98.0	98.7				
HAL		98.9	99.0	99.2	99.3	99.3
COD		98.9	97.6	F	99.1	98.6
ATF						

Table 3.3. Parameter estimates, and corresponding coefficients of variation (CV) for the (A) base model and selected models with and without autocorrelation and having (B) one, (C) two, or (D) three ecological parameters.

Models with autocorrelation [a]												
α_1		α_2		α_3		β		φ		γ parameter		
Est.	CV	Est.	CV	Est.	CV	Est.	CV	Est.	CV	Effect	Est.	CV
A. Base Model												
0.38	0.58	0.03	0.45	0.33	0.32	2.7×10^{-5}	1.10	0.45	0.27	None		
B. One Ecological Parameter												
0.10	0.55	0.03	0.32	1.42	0.40	4.3×10^{-5}	0.46	0.17	0.55	COD-2	-1.53	0.32
0.11	0.53	0.03	0.32	1.17	0.38	4.2×10^{-5}	0.46	0.16	0.95	COD-3	-1.39	0.23
C. Two Ecological Parameters												
0.08	0.60	0.02	0.36	1.61	0.44	5.2×10^{-5}	0.53	0.24	0.67	COD-2	-1.67	0.22
										CLD-0	0.33	0.36
0.09	0.58	0.03	0.35	1.29	0.40	4.3×10^{-5}	0.52	0.21	0.78	COD-3	-1.51	0.23
										CLD-0	0.32	0.37
D. Three Ecological Parameters												
0.06	0.62	0.02	0.38	1.70	0.44	3.9×10^{-5}	0.68	0.26	0.70	COD-2	-1.63	0.23
										CLD-0	0.38	0.32
										DCG-0	-0.27	0.45

[a] Parameters are defined in Table 3.1. The number following the dash in the γ parameter indicates the red king crab age, in years, when the parameter effect is assumed to occur. For example, COD-2 represents the correlation of Pacific cod abundance lagged to affect age-2 crab. Brood years are 1964–1974 for α_1, 1975–1984 for α_2, and 1985–1999 for α_3.

Table 3.3. (continued)

α_1		α_2		α_3		β		φ		γ parameter[a]		
Est.	CV	Est.	CV	Est.	CV	Est.	CV	Est.	CV	Effect	Est.	CV
Models without autocorrelation												
B. One Ecological Parameter												
0.09	0.83	0.02	0.28	1.49	0.46	4.1×10^{-5}	0.44	NA		COD-2	-1.56	0.22
0.10	0.62	0.03	0.32	1.24	0.42	4.1×10^{-5}	0.44	NA		COD-3	-1.44	0.22
C. Two Ecological Parameters												
0.07	0.59	0.02	1.70	0.29	0.37	3.5×10^{-5}	0.46	NA		COD-2	-1.70	0.17
										CLD-0	0.30	0.42
0.08	0.52	0.03	0.22	1.40	0.47	3.5×10^{-5}	0.43	NA		COD-3	-1.59	0.17
										CLD-0	0.30	0.38
D. Three Ecological Parameters												
0.05	0.72	0.02	0.29	1.81	0.33	2.6×10^{-5}	0.58	NA		COD-2	-1.65	0.19
										CLD-0	0.35	0.35
										DCG-0	-0.29	0.54
0.06	0.59	0.02	0.27	1.63	0.37	3.0E-05	0.50	NA		COD-2	-1.82	0.17
										CLD-0	0.24	0.50
										WS3-0	0.28	0.56

(AIC_c = 98.9) or the non-autocorrelated COD-3 models (AIC_c =98.3) because the AIC_c values of these two models differed by ≤ 2. Therefore, these Pacific cod anomalies were all examined as the first parameter of two ecological parameter models. We also noted that the non-autocorrelated COD-2 model showed only weak improvement over models with a single ecological parameter of COD-1, COD-4, or COD-5 without autocorrelation and the autocorrelated COD-3 (Table 3.2). Among models incorporating a second ecological parameter, weak model improvement was indicated by inclusion of CLD-0 with COD-2 without autocorrelation (AIC_c = 94.5; Table 3.2), although fit of this model based on AIC_c values did not differ from non-autocorrelated models of COD-2 with WS3-0 or COD-3 with CLD-0, or from autocorrelated CLD-0 with either COD-2 or COD-3. Configurations with three ecological parameters that reduced the AIC_c value from the non-autocorrelated COD-2 with CLD-0 model included: non-autocorrelated models of COD-2 and CLD-0 with either DCG-0 (AIC_c = 92.6) or WS3-0 (AIC_c = 94.6) and COD-3 with CLD-0 and DCG-0 (AIC_c = 94.9); and the autocorrelated COD-2 with CLD-0 and DCG-0, but AIC_c differences of < 2 from the best two-parameter model suggested that model fits were not credibly different (Table 3.2). Models with four ecological parameters showed no improvement in AIC_c values.

Among models with the smallest AIC_c values for a given number of ecological parameters, the Pacific cod coefficient was consistently and strongly negative, ≤ -1.51 among the better fits within a parameter group, and exhibited reasonably good estimated precision (CVs generally ≤ 0.25; Table 3.3). The coefficient for cloud cover ($\gamma = \sim 0.35$)

as a secondary ecological factor was weakly positive and again with reasonable precision (CVs of 0.36–0.37; Table 3.3). There is a weak indication that either freshwater discharge (DCG-0) or wind speed cubed (WS3-0) may be important, but there is also high uncertainty in these estimates.

Thus, it is apparent that Pacific cod is a primary component in the optimal model configuration. In general, Pacific cod reduced overall variability by > 20% compared to the base model with autocorrelation and no ecological factors (Table 3.4). Cloud cover may also be important, albeit to a lesser extent than Pacific cod; inclusion of cloud cover further reduced variability by about 8–10%. Inclusion of additional factors beyond these components is less definitive, with substantially reduced precision in the parameter estimates, tending to increase the likelihood of spurious correlations. On this basis, the optimal model included COD-2 and CLD-0 as ecological parameters in a lag-5 Ricker model without autocorrelation, although the consideration of these factors in an autocorrelated model cannot be ruled out.

With the incorporation of ecological parameters, several notable patterns emerged in some of the other parameter estimates. For example, per-capita productivity decreased from 0.38 to ≤ 0.11 for the 1964–1974 brood years (α_1) and increased substantially from 0.33 to > 1.17 for the 1985–1999 brood years (α_3; Table 3.3). Inclusion of ecological factors also resulted in increased density dependence in models with an autocorrelation term, but a decrease or unchanged in models without autocorrelation. Increased

Table 3.4. Summary of number of estimated parameters (p), residual sums of squares (RSS), peak spawner abundance (S_p), RSS reduction, and peak recruit abundance (R_p) for brood years 1964–1974, 1975–1984, and 1985–1999 for selected models (A) with and (B) without autocorrelation among different tiers of ecological effects.

Ecological Parameters	p	RSS	Reduction	S_p	R_p by brood year 1964–1974	1975–1984	1985–1999
A. Autocorrelated models							
Base	5	29.0	NA	37,586	14,386	1,066	12,276
COD-2	6	21.4	26.2%	23,367	5,117	257	2,591
COD-3	6	22.4	22.9%	23,555	5,156	256	2,628
COD-2,CLD-0	7	17.8	38.6%	21,698	4,874	245	2,392
COD-3,CLD-0	7	18.9	34.8%	23,035	4,957	251	2,564
COD-2, CLD-0, DCG-0	8	15.3	47.1%	25,828	5,018	275	2,809
B. Models without autocorrelation							
None	4	36.0	124.1%	32,769	5,825	318	3,684
COD-2	5	22.1	24.0%	24,233	807	222	13,288
COD-3	5	22.9	21.0%	24,353	938	304	11,093
COD-2,CLD-0	6	18.9	34.7%	28,430	685	224	17,765
COD-3,CLD-0	6	19.8	31.9%	28,581	797	316	14,722
COD-2,CLD-0, DCG-0	7	16.4	43.6%	38,299	740	282	25,468
COD-2,CLD-0, WS3-0	7	17.3	40.3%	33,452	786	259	20,104

[a] Ratio of the residual sums of squares relative to the base model compared.

productivity and density dependence are also exhibited in the slightly more pronounced dome-shape of the S-R curves with additional ecological factors (Figure 3.3). The autocorrelation coefficient also decreased from 0.45 with no ecological parameters to $\leq$ 0.26 with ecological factors. Based on that aspect, and looking at patterns in model fits, it is apparent that the ecological factors provided substantial explanatory associations in the models lacking an autocorrelation parameter (Figure 3.4). Finally, peak spawning biomass, S_p, declined substantially from 37.6 million males under the base model, to a range of 21.7 to 28.5 million males in most models that included ecological parameters, although models with three ecological parameters and lacking autocorrelation still had relatively high S_p values (Table 3.4; Figure 3.3).

Trends in ln(R/S) residuals show relatively small, incremental improvement in model fit by inclusion of one and two ecological parameters (Figure 3.3). In particular, augmenting the base model with a single ecological parameter of COD-2 generally reduced positive residuals in the late 1960s and mid 1970s and negative residuals during the 1980s. Inclusion of CLD-0 as a second improved model fit for only a few brood years, such as 1969 and 1981, but residuals also increased in some years, such as 1988.

Because of the prevalence of Pacific cod as an ecological association and greater complexities and uncertainties with the inclusion of additional ecological factors, we ran the MSC analysis based on the COD-2 model (Table 3.5; Figure 3.5). Results showed substantial variability in the estimated stock abundance level associated with maximum

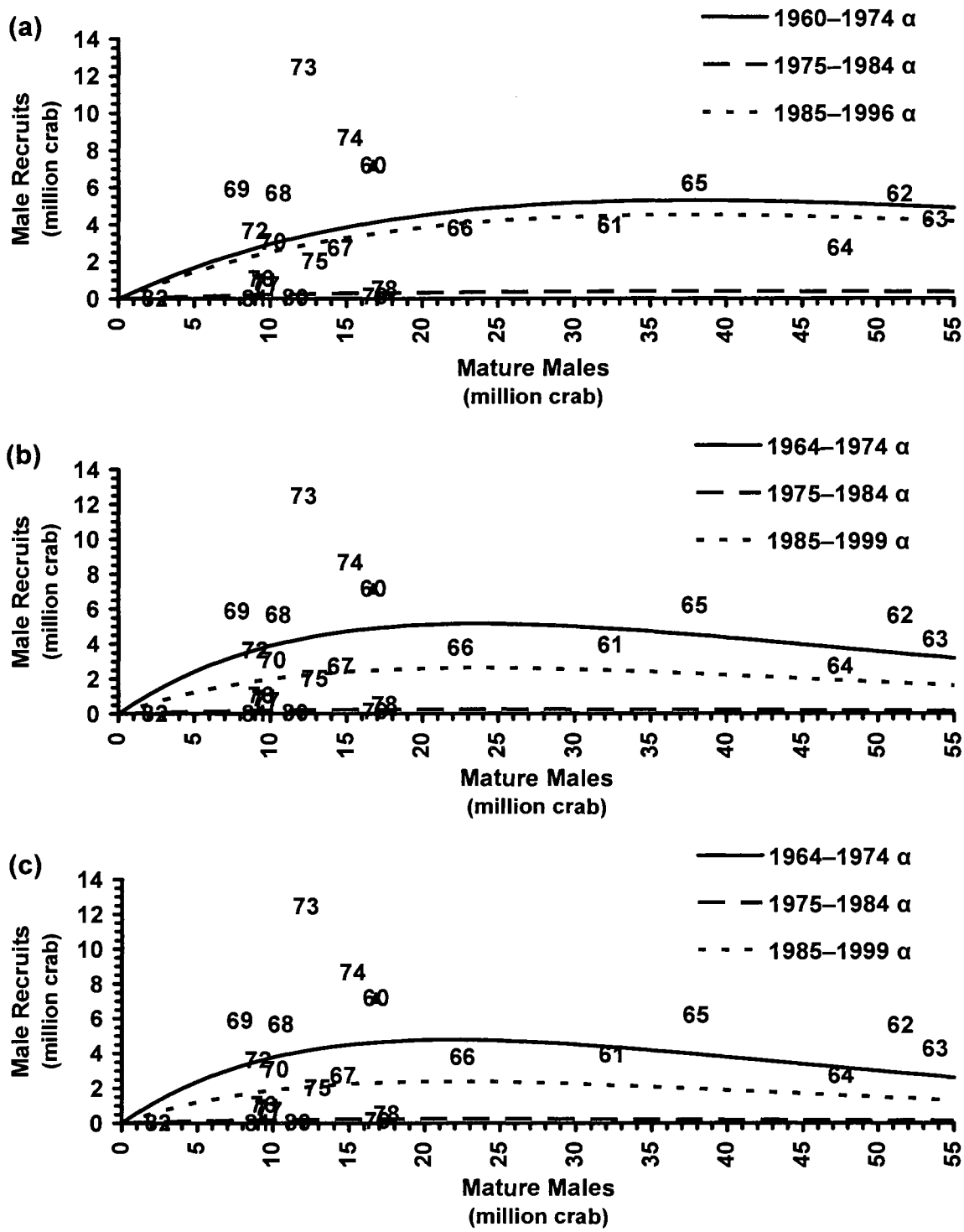

Figure 3.3. Spawner-recruit models configured with (a) no (base model), (b and d) one (COD-2), and (c and e) two (COD-2 and CLD-0) ecological parameters showing differences in productivity for the 1964-1974, 1975-1984, and 1985-1999 brood years; models d and e lack an autocorrelation parameter.

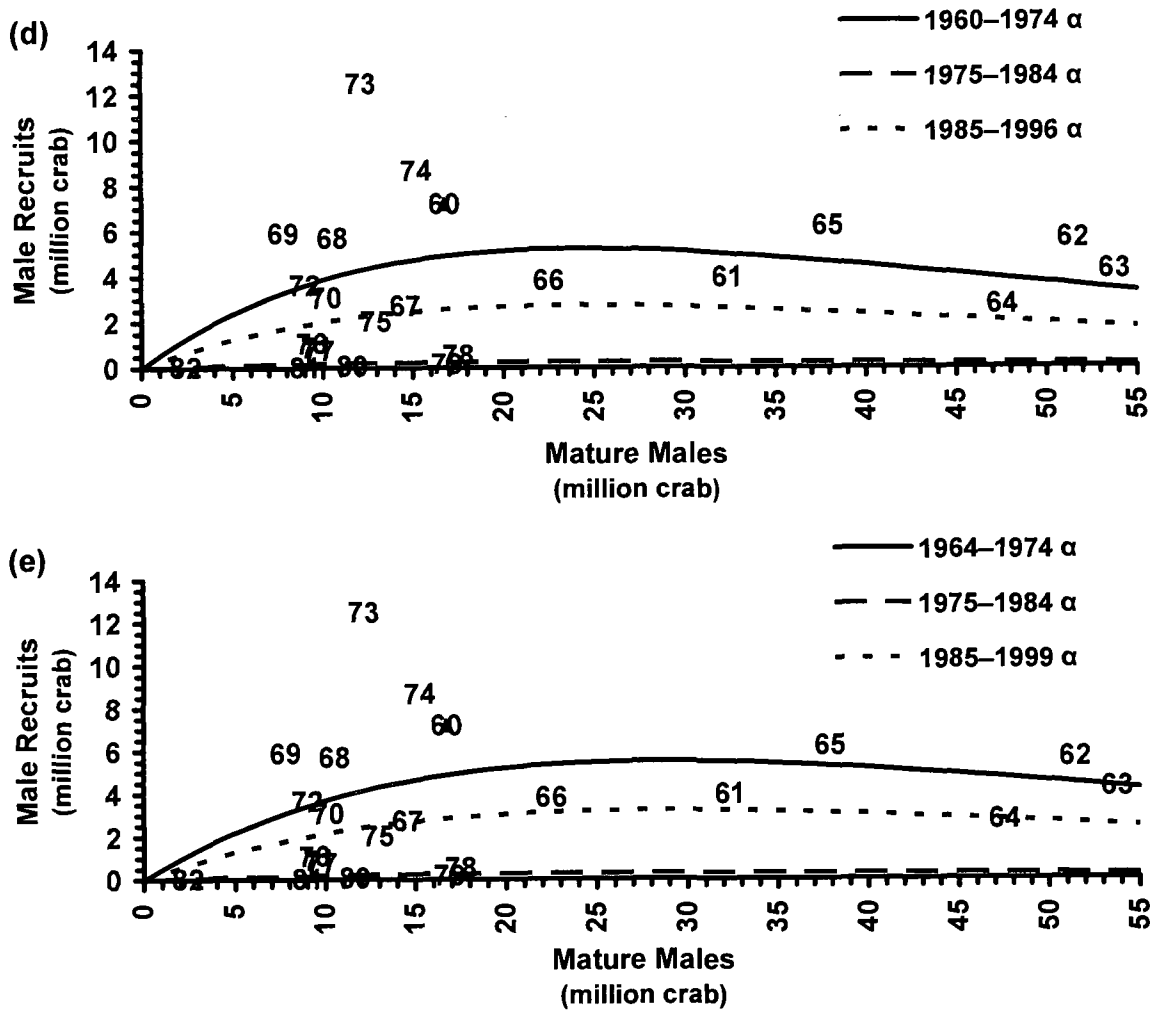

Figure 3.3. (continued)

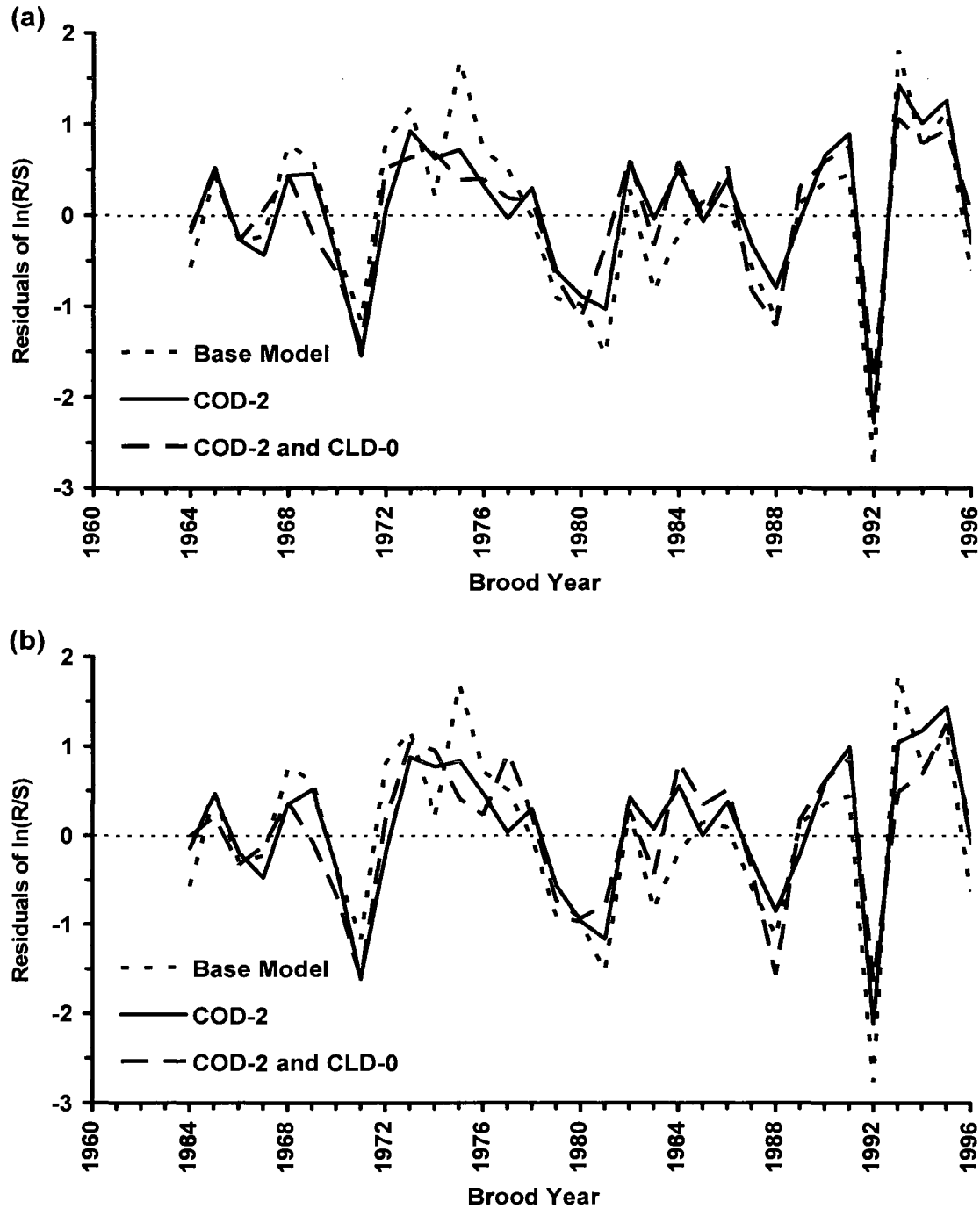

Figure 3.4. Trends in ln(R/S) residuals among models (a) with and (b) without autocorrelation configured with no (autocorrelated base model), one (COD-2), and two (COD-2 and CLD-0) ecological parameters.

Table 3.5. Estimates of male spawners, S_m, recruits, R_m, and catch, C_m, in thousands of males, and the exploitation rate, μ_m, at maximum sustainable catch under assumed values of productivity and density dependence and at three quartiles of the distribution of Pacific cod biomass.

Parameter[a]	1st Quartile	Median	3rd Quartile
α	1.49	1.49	1.49
β	4.13E-05	4.13E-05	4.13E-05
COD-2	-1.09	0.38	1.07
γ	-1.56	-1.56	-1.56
α'	8.072	0.819	0.281
S_m	17,939	None	None
R_m	69,066	None	None
C_m	51,128	None	None
μ_m	0.711	None	None

[a] "None" substituted for nonsensical solutions (e.g., S_m or $R_m < 0$).

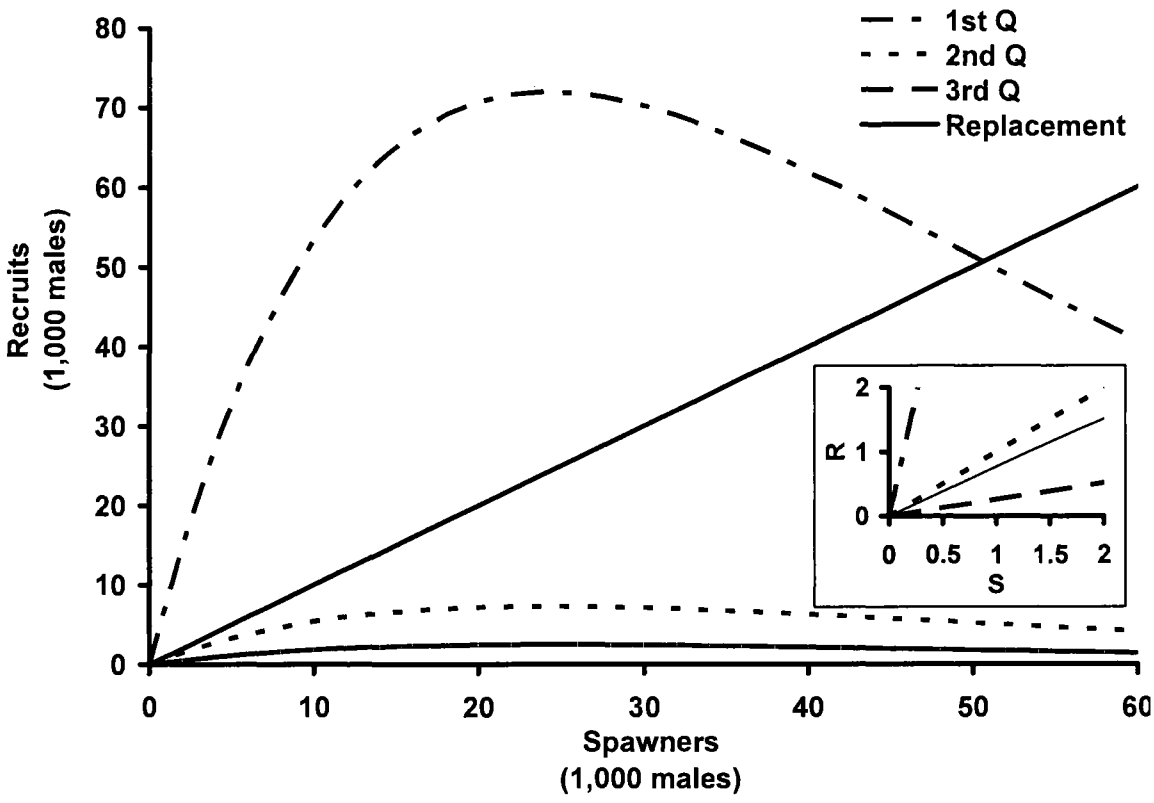

Figure 3.5. Spawner recruit curves based on alpha and beta parameters for the 1985–1999 brood years and showing separate curves for each of the first three quartiles of the distribution Pacific cod anomalies. The inset shows the origin.

sustained catch under the current productivity and density dependence parameters. Essentially, there is no surplus production available at the median and third quartile of the distribution of Pacific cod anomalies. But, substantial catch is available if the first quartile of Pacific cod anomalies is assumed. Productivity at the origin also shows substantial recruitment associated with the first quartile of Pacific cod anomalies, and productivity marginally above replacement associated with the second quartile of anomalies (Figure 3.5 inset). The productivity associated with the third quartile of anomalies appears to be insufficient to attain replacement.

3.6 Discussion

Previous studies found a strong relationship between red king crab recruitment and ecological factors operating on the larval crab stage (Zheng and Kruse 2000, 2003). In contrast, we found the most prominent factor around Kodiak Island to be a consistent and a strong negative relationship between age-3+ Pacific cod biomass in the Gulf of Alaska and post-larval red king crab, with the strongest association for age-2 crab (Table 3.4). Inclusion of Pacific cod anomalies, particularly COD-2 or COD-3, into the S-R model for Kodiak red king crab substantially improved model fit compared to other models considered with a single ecological parameter (Table 3.4). The COD-2 and COD-3 models also provided a better fit than our base model, an autocorrelated Ricker model

(AIC_c = 106.8), similar to that in Bechtol and Kruse (*in press* b) but limited to brood years 1964–1999.

While the mechanism of a negative relationship between juvenile king crab and Pacific cod cannot be confirmed from our analysis, predation on juvenile crab is most likely. Shallow nearshore waters are particularly important as rearing habitat for early juvenile stages of red king crab, but at about 1–2 years after settlement, red king crab become less solitary and begin to form pods as they move from shallow nearshore environments around Kodiak to deeper waters. Although crab cannot be aged, growth of juvenile red king crab is believed to be approximately linear up to 60 mm CL for both males and females, with a mean length of 13 mm and 33 mm after the first and second years of life, respectively (McCaughran and Powell 1977). Juvenile king crab at these sizes would certainly be vulnerable to predation by Pacific cod and other predatory fishes, and crab at these and larger sizes would also be vulnerable during the soft-shell phase of their molt. Predation impacts on king crab likely intensified around Kodiak Island in response to the general increase in the predator biomass observed in the Gulf of Alaska during the 1970s (Hollowed and Wooster 1992; Anderson and Piatt 1999; Hare and Mantua 2000; Ciannelli et al. 2005). However, there has been little documentation of predation on any king crab life stage (Albers and Anderson 1985; Livingston 1989; Yang 1993; Dew and McConnaughey 2005; Yang et al. 2006; Zheng and Kruse 2006). Blau (1986) noted that only 77 of the 12,443 Pacific cod stomachs examined during ADF&G pot surveys around Kodiak during 1972-1983 contained king crab. The lack of evidence of fish predation is

likely results from systematic biases in the collection of diet data due to several factors: (1) few groundfish stomachs were historically sampled in nearshore, shallow waters inhabited by juvenile crab; (2) predator stomachs have typically been sampled from deeper waters in summer, not during late winter to spring when most adult crab undergo ecdysis and are most vulnerable to predation; and (3) extensive collection of diet data in recent years occurred when red king crab abundance is extremely low relative to alternative prey.

A spatial analysis of pot survey data shows strong increases in relative abundance of Pacific cod in nearshore waters around Kodiak at a time when the king crab population drastically declined (Figure 3.6). Moreover, as king crab abundance declined, the crab population concentrated into nearshore areas as the centers of preferred habitat (Johnson 1990), perhaps as a density-dependent response (MacCall 1990). Anderson et al. (1997) suggested that warmer temperatures allowed cod to remain in inshore bays throughout winter, instead of migrating offshore as nearshore areas cooled. If true, this could have altered the functional predator-prey response between these two species. In the eastern Bering Sea similar increases in near-bottom temperature resulted in changes to the spatial distribution of Pacific cod to the apparent detriment of the snow crab population, and the biomasses of yellowfin sole *Pleuronectes asper* and Pacific cod show significant inverse relationships with red king crab recruitment (Zheng and Kruse 2006).

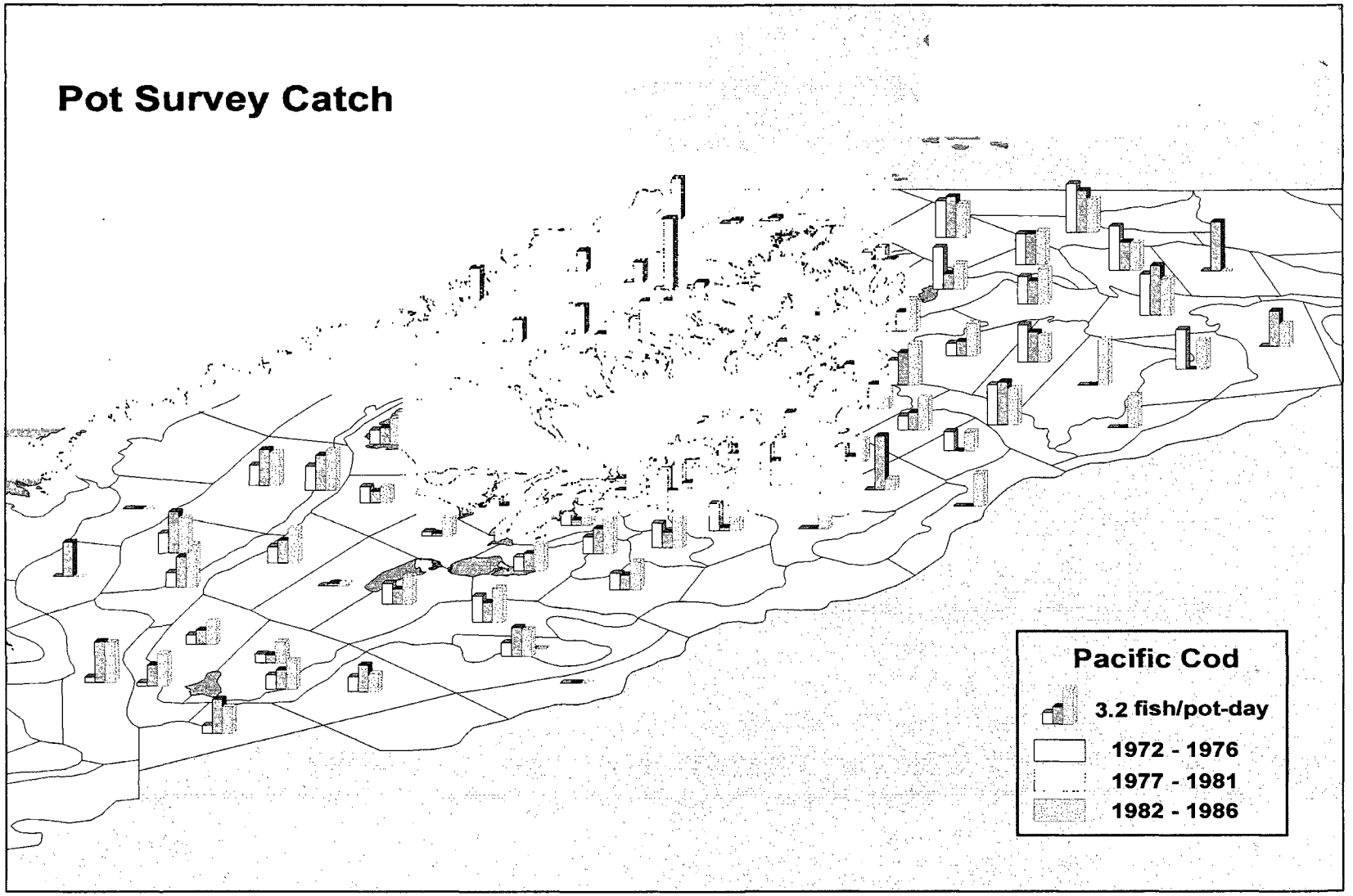

Figure 3.6. Distribution of Pacific cod in the ADF&G pot survey for three periods during 1972–1986.

Changes in Pacific cod biomass and distribution have also been linked to the collapse of northern shrimp *Pandalus borealis* populations in the Gulf of Alaska. For instance, a retrospective analysis found a strong increasing trend of natural mortality resulted in the crash of the northern shrimp stock in Kachemak Bay during the 1980s (Fu et al. 1999).

A corresponding trend of increasing trawl survey catches of cod further suggests that intensified cod predation was likely responsible for the shrimp decline in Kachemak Bay (Fu and Quinn 2000). Perhaps not coincidentally, an examination of Pacific cod stomachs suggested that cod predation caused the decline of a lightly fished stock of northern shrimp in Pavlof Bay, Alaska (Albers and Anderson 1985).

Nevertheless, cod predation alone cannot explain Kodiak red king crab population dynamics. We suggest that increased Pacific cod abundance in the Kodiak area in the early 1980s further compromised an already depleted red king crab population. Very high harvest rates in the late 1960s were associated with stock decline due to both direct fishery removals and subsequent reproductive failure associated with sex ratios skewed toward females (Bechtol and Kruse *in press* a). Undoubtedly, environmental factors also played a role in the recruitment failures. Thus, the late 1970s increase in Pacific cod abundance, coupled with a temperature-driven nearshore shift in cod spatial distribution, likely increased crab predation, thereby exacerbating a decline in crab abundance originally triggered by fishing and other causes.

Although ecosystem response to environmental forcing is likely nonlinear (Hare and Mantua 2000), other evidence exists for roles of climate-driven changes in the physical environment on groundfish populations in the Gulf of Alaska and eastern Bering Sea. For example, Quinn and Niebauer (1995) found strong pollock recruitment in the eastern Bering Sea to be correlated with above normal air and bottom temperatures and reduced sea ice cover, factors that promote zooplankton production. Although sea ice is not a factor in the Gulf of Alaska, the pre-1976 regime was associated with low sea surface temperature and low biomasses of predatory groundfish, such as flatfishes and Pacific cod. During and immediately after the 1976 regime shift, a period of high sea surface temperature favored strong zooplankton production in the Gulf of Alaska, supporting strong pollock recruitment in the presence of continued low groundfish predation (Bailey 2000; Ciannelli et al. 2005). However, high zooplankton populations seem to have been detrimental to phytoplankton needed for first-feeding red king crab zoea, resulting in reduced crab recruitment, particularly beginning in the early 1980s (Figure 3.2). Although sea surface temperature declined in the decade following the regime shift, ecosystem "maturation" resulted in increased biomass of predatory fishes, particularly Pacific halibut, arrowtooth flounder, flathead sole *Hippoglossoides elassodon*, and Pacific cod (Bailey 2000), further constraining recruitment. Since the 1989 regime shift, the ecosystem has been generally characterized by moderate sea surface temperature, but relatively high groundfish biomass (Hare and Mantua 2000; Mueter and Norcross 2002; Ciannelli et al. 2005). Thus, ocean temperature changes associated with the 1976 regime shift had substantial, but opposite, effects on the prey of red king crab compared to

groundfishes, including Pacific cod. As a result, a compromised feeding environment for larval red king crab was coupled with intensified groundfish predation on juvenile crab.

Crab predators are not limited to groundfish species, although data on populations such as marine mammals are also sparse. For example, sea otters *Enhydra lutris* have been observed feeding on red king crab and Kvitek et al. (1992) documented restructuring of benthic habitat by an expanding sea otter distribution along the north shore of Kodiak Island in the 1980s; the intensity of habitat disturbance was related to the temporal gradient of sea otter occupancy. However, there are few long-term data on the spatial distribution and abundance of sea otters around Kodiak.

We also considered the greater scale of benthic habitat loss or restructuring, and associated crab discard mortality associated with the bottom trawl fishery for shrimp which operated in the Kodiak area from the 1950s until 1986. However, analysis of the relationship between the shrimp fishery and red king crab recruitment was inconclusive due to the inconsistency in the data time series. Additional fisheries historically occurred in the Kodiak area, notably the foreign fisheries targeting groundfish prior to implementation of the Exclusive Economic Zone in the mid-1970s. These fleets could legally fish up to 12 nautical miles from shore and likely had an impact on benthic habitat and organisms, including red king crab, but records on catch and discards are difficult to obtain and were not included in our analysis.

Secondary ecological effects of air temperature, wind speed cubed, freshwater discharge, and sea surface temperature, showed no improvement over the model with a single ecological factor of COD-2 (Table 3.2). However, improved model fit with the inclusion of cloud cover as a secondary ecological factor was somewhat unexpected, because of the seemingly contradictory effects of cloud cover; reduced cloud cover increases the incidental light to the benefit of photosynthetic phytoplankton, but also increases the water temperature to the benefit of zooplankton (Weingartner 2007). We interpret our results to mean that a reduction in zooplankton predation pressure has a greater effect than the reduction in light for the phytoplankton serving as forage for larval crab larvae. Another possibility is that zooplankton prey on crab larvae and that increased cloud cover reduced that predation pressure. Of course, the apparent effect of cloud cover could also be spurious. In any case, inclusion of cloud cover led to a minor improvement over our best single ecological parameter models based on cod biomass.

The role of currents on larval advection and/or retention may be important, but they are difficult to study in the Kodiak Archipelago. The ACC is the primary ocean current in the area, but bathymetric features such as troughs and canyons can also affect localized flow patterns, including the formation of cyclonic eddies within embayments that facilitate larval retention (Allen et al. 2001; Stabeno et al. 2004). Increased freshwater discharge in the Gulf of Alaska not only increases mean current flow that could sweep larvae away from nursery areas, but also promotes eddies and other current instabilities that could lead to greater retention of crab larvae (Okkonen et al. 2003; Weingartner 2007). So, it is not

clear whether increased flow in the ACC is deleterious or advantageous to crab larval retention. Such ocean features tend to be highly localized, spatially and temporally, and a detailed analysis of their potential effects on long-term population recruitment is beyond the scope of our present study.

Our study is not without typical statistical limitations. Although the use of AIC_c values provides a means to compare the relative fit of competing models (Burnham and Anderson 2004), our analysis found several model configurations produced similar AIC_c values. Pacific cod, particularly COD-2, was an important ecological factor in all models, and a large portion of the more complex models included CLD-0; the benefits of including other ecological factors were less clear. Given these aspects, combined with the recognition that a simpler model is less prone to spurious associations, a preferred model including COD-2 and CLD-0 is justified.

We also note that interpretation of the best model depends on the candidate models selected for comparison (Peterson et al. 2003). For example, had we not considered cod in our candidate set, the best fit with a single ecological parameter was POL-0, also showing strong improvement over our base model. Populations of pollock and Pacific cod both exhibited substantial increases in biomass in the Gulf of Alaska following the mid 1970s regime shift, but the subsequent ecosystem maturation appears to have had a somewhat negative effect on pollock versus a benefit on Pacific cod based on biomass

trends (Bailey 2000; Ciannelli et al. 2005). As a result, biomass trends for these two species are consistent for some years and opposite for other years in the time period considered by our analysis, perhaps explaining why Pacific cod provided a better fit than pollock.

Alternative datasets beyond those we considered may have provided a stronger inference into red king crab population dynamics around Kodiak Island. But we also recognize that consideration of additional variables increases the potential for spurious associations. We have attempted to include variables that are biologically meaningful, subject to the limitation of being a reasonably long-time series. Whereas several studies have explored relationships between various ecosystem components in the Gulf of Alaska (Hollowed and Wooster 1992; Anderson and Piatt 1999; Hare and Mantua 2000; Ciannelli et al. 2005; Mueter et al. 2007), the lack of long-term datasets has limited such analyses. Availability of long-term ecological datasets similarly constrained our analysis of Kodiak red king, a population that was fished heavily in the 1960s during a period of relatively high crab abundance (Figure 3.2). However, there is a paucity of oceanographic observations prior to the 1970s, and red king crab abundance was already well into decline after oceanographic and stock assessment data were being systematically collected. In addition, the effect of short-term events on red king crab recruitment is difficult to assess but cannot be ruled out. For example, the 1964 Good Friday Earthquake caused substantial damage to intertidal and shallow subtidal communities

throughout southcentral Alaska (Spies 2007), but the impact on red king crab recruitment is difficult to assess.

In summary, we found a strong negative relationship between Gulf of Alaska biomass of age 3+ Pacific cod and recruitment of Kodiak red king crab, with the postulated causative mechanism being predation. Incorporation of Pacific cod biomass into the stock-recruit model substantially reduced the crab abundance estimated to produce peak recruitment (Table 3.4). Taken together, our research suggests the complicit effects of at least three key factors in the decline of Kodiak red king crab and the failure to recover: (1) stock depletion from high harvest rates in the late 1960s (Bechtol and Kruse *in press* a); (2) compromised reproductive potential associated with resultant low stock size (Bechtol and Kruse *in press* a, *in press* b); and (3) intensified predation owing to increased cod biomass beginning in the 1980s and nearshore shifts in both the crab serving as prey (density-dependent response) and their groundfish predators (temperature response). The potential additional mechanism indexed by cloud cover is less clear and requires further investigation; it may signal a switch in conditions favoring zooplankton (prey of groundfish larvae) over phytoplankton (diatom prey of red king crabs), but alternatively it may be spurious. Thus, we offer here a relatively coherent scenario of the role of fishing, climate, and ecological factors on the decline of Kodiak red king crab as a point of departure for future investigations.

Our research has implications on ecosystem approaches to fishery management in the Gulf of Alaska. Namely, fishery management should particularly include the apparent negative influence of Pacific cod on red king crab recruitment. Experiments are underway to evaluate the ability of crab hatcheries to rehabilitate red king crab in the Gulf of Alaska. The effectiveness of such rehabilitation efforts, if implemented, may depend on the ability of enhancement efforts to increase king crab production sufficiently to swamp cod predation, which appears to be a current bottleneck to crab recovery. Although cod biomass has been declining since the mid 1980s, warm temperatures continue to favor a nearshore geographic distribution of these predators, perhaps to the detriment of the recovery of red king crab stocks.

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General Conclusions

The intent of this study was to improve understanding of the conditions surrounding the rise, collapse, and continued depressed status of the red king crab stock around Kodiak Island. Research was directed toward three primary objectives: (1) reconstructing the king crab spawning stock abundance and recruitment over 1960 to 2004; (2) estimating a stock-recruit relationship; and (3) identifying potential influences of biotic and abiotic factors on crab recruitment. As with all retrospective analyses, the results of this study were constrained by the length and types of data available for analysis. For instance, fishery independent data on red king crab were not collected until well after this stock peaked in abundance during the mid 1960s, thereby prohibiting a meaningful analysis of density-dependent effects during an important period in the history of this stock. Moreover, the lack of female data during this period of peak population abundance severely constrains the ability to estimate historical abundances of females for stock-recruit analyses. Nevertheless, study results offer substantial insight into the history of the Kodiak red king crab stock.

Reconstruction of stock abundance revealed that the rapid fishery expansion during the 1960s coincided with, and was supported by, exceptionally strong crab year classes, likely resulting from optimal environmental conditions in the late 1950s. However, as harvest rates increased, crab recruitment declined such that increasing fishing pressure

was being placed on a declining male population. Through the 1970s, the fishery developed a greater reliance on males that were newly recruited to legal size, providing less resilience to the population as a few strong year classes continued to support the fishery. Concurrently, sex ratios became skewed toward females and reproductive failure likely occurred for portions of the female population owing to insufficient males for mating. An important spatial feature of this fishery was the expansion from bays to offshore grounds during the 1960s and 1970s as catch rates in nearshore areas declined.

The stock-recruit analysis provides additional evidence for shifts in stock productivity over the time series. The optimal stock-recruit model was an autocorrelated Ricker model using: (1) all males as the spawner currency; (2) a 5-year lag between spawning and recruitment; and (3) separate productivity parameters to represent brood years of 1960–1974, 1975–1984, and 1985–1996. Because the spawner time series started with the 1960 brood year, the high recruitments observed in the early 1960s resulted from reproduction in the 1950s that could not be included in the analysis. However, the optimal results of an all male currency and a 5-year lag both indicate the important reproductive contribution that smaller mature males have made to the population beginning with the 1960s brood years. A strong reproductive contribution by sublegal males is symptomatic of the occurrence of a recruit fishery in the time series and reduced resilience in the population. The autocorrelated aspect of the Ricker model indicates a strong serial component to crab recruitment patterns -- good years follow good years, bad years follow bad years – with

transitions in potential recruitment further associated with three different periods of productivity.

The decline in stock abundance corresponded with a severe constriction in geographic distribution to just a limited number of nearshore areas around Kodiak Island. Recruitment failures in the 1980s further contributed to this limited spatial distribution. Although not confirmed by the analysis, the limited distribution of adult crab may have caused depensation in the stock-recruit relationship, making it very difficult for the stock to recover despite a commercial fishery closure since 1983. However, depensation remains difficult to prove.

A climate regime shift in the late 1970s triggered dramatic ecosystem changes that likely had adverse effects on crab recruitment. In particular, increased ocean temperatures facilitated a greater abundance of predatory fishes, such as Pacific cod, and also a shift in cod distribution towards nearshore waters, the same areas occupied by the largest component of the depressed red king crab population. Thus, I propose that the combined effects of very low reproductive potential and unfavorable environmental conditions have contributed to the depressed status of this stock for the past 25 years. Because ecosystem changes tend to be nonlinear, a variety of factors will likely need to occur in concert if the abundance of red king crab around Kodiak Island is to exhibit a substantive increase in the future.

The first of these factors is that larval crab must encounter environmental conditions that facilitate strong survival, namely a stratified and stable water column and moderately cool water temperatures. Second, those crab surviving to the benthic stage must be of a sufficient abundance to saturate potential predator populations. Additional studies are likely needed to develop a quantitative understanding of the impact that potential predators have on juvenile red king crab and the abundance of crab that is needed in order to saturate the predator population. Third, these events must occur over a series of years in order to develop a broad age/size distribution that increases the resiliency of the red king crab population. Finally, fisheries management strategies must provide a conservative approach that recognizes the importance of a broad size/age distribution in the crab population and provides for an expansion of the spatial distribution of the population by limiting the potential for localized overharvesting. A first step would be a comprehensive management strategy evaluation to ascertain the optimal approaches to the fishery for Kodiak red king crab given our current knowledge of crab biology, changes and interactions among ecosystem components, and the precautionary principle.

Appendices

Appendix A. Ecology and Crab Early Life History

A.1 Ecological Factors Affecting Red King Crab Early Life History

A summary of red king crab life history is important to understanding potential effects of biotic and abiotic factors on crab recruitment. Unless otherwise specified, much of following life history information is summarized from Tyler and Kruse (1995), NPFMC (1998), Zaklan (2002), and Donaldson and Byersdorfer (2005). The factors discussed here are focused on early life history in red king crab, particularly the first four to five years of a crab's life.

Annual reproduction by red king crab around Kodiak is closely tied to molt timing. Adult males molt as early as December, but begin to "skip molt" in some years after reaching approximately 125 mm carapace length (CL) (McCaughran and Powell 1977), whereas adult females molt and mate annually from March through April. Mating is typically earlier in years with warmer water temperatures and for primiparous (first-time mating) females (Shirley et al. 1990). Eggs are fertilized and then incubated on the female's abdomen for approximately 300 d. During egg development, exposure to prolonged temperatures outside a range of 2° to 5° C are assumed to increase egg mortality through: (a) disease or parasites; and (b) development rates that result cause hatch timing to mismatch with the spring bloom (Sparks and Morado 1985; Blau 1986; Otto et al. 1990;

Kuris et al. 1991). Embryos hatch during March though May, and larvae inhabit the water column at depths < 100 m. Larvae pass through four zoeal stages, lasting approximately two weeks each, and then metamorphose into a glaucothoe stage, although stage duration varies with hatch date and water temperature (Shirley and Shirley 1989).

Ocean current speed and direction affect spatial patterns in larval settlement; currents advecting larvae away from preferred nearshore nursery habitats likely reduce crab larval survival. Ocean currents in the Gulf of Alaska primarily include the counterclockwise Alaska Gyre in the ocean basin and the Alaska Coastal Current (ACC), which dominates coastal waters over the continental shelf as it flows from the Columbia River to the Bering Sea (Reed and Schumacher 1986; Stabeno et al. 2004; Royer and Grosch 2007; Weingartner 2007a). The intensity of the ACC around Kodiak varies seasonally and spatially, particularly due to water stratification dependent on freshwater runoff and wind-mixing (Weingartner et al. 1995). However, advection varies on a fine scale, spatially and temporally, partly due to eddies, making reconstruction of historical effects difficult.

Larval feeding and growth also govern survival. Newly hatched zoea must feed within 2-6 d after hatching, so availability of suitable prey is critical for survival (Paul et al. 1989). Early instar zoea tend to be phytoplanktivorous, preferring the diatom *Thalassiosira* sp., but becoming more zooplanktivorous in later stages (Shirley and Shirley 1989).

Several physical and biological factors may regulate feeding success of larval red king crab. Based on studies in Auke Bay, Alaska, a stable water column during the spring bloom favors a phytoplankton community dominated by *Thalassiosira* sp. (Ziemann et al. 1990; Bienfang and Ziemann 1995). Strong stratification prevents mixing beyond the euphotic zone and promotes the spring phytoplankton bloom, whereas weak stratification is associated with a deeper mixed-layer depth and low phytoplankton densities in the euphotic zone (Stabeno et al. 2004; Weingartner 2007a). Seasonal maxima of rainfall and solar heating during May to August increase freshwater runoff and promote water column stratification, whereas strong winds induce deep vertical mixing (Weingartner et al. 1995). However, relatively warm sea surface temperature also promotes zooplankton production, particularly copepods, such as *Pseudocalanus* (Smith and Vidal 1984), which forage on phytoplankton. Thus, a combination of weak winds that facilitate water column stratification during the spring phytoplankton bloom, and relatively cool temperatures that promote a plankton community dominated by *Thalassiosira* diatoms during March through June, should favor feeding and survival of red king crab larvae. Phytoplankton production is also tied to changes in incident light during spring, so a more extensive spring cloud cover could delay and reduce the spring bloom (Bienfang and Ziemann 1995; Tyler and Kruse 1995; Cooney 2007). Cloud cover is also inversely related to the warming of the surface water due to constraints on the amount of solar radiation available to heat the upper ocean (Weingartner 2007a).

Strong seasonality and interannual variability are two of the important time scales in atmospheric forcing and oceanography. Environmental influences on time scales of two to seven years are driven by the El Niño-Southern Oscillation (ENSO). Positive anomalies in winter air temperature, precipitation, alongshore winds, and sea level are typically associated with El Niño events and negative anomalies in these factors with La Niña events. These ENSO events typically develop near the equator in spring with a maximum Gulf of Alaska effect 8 to 12 months later in the fall and winter (Weingartner 2007b). Climate regime shifts are associated with decade-scale oceanic variability in winter indexed by the Pacific Decadal Oscillation (PDO), which describes anomalies in sea surface temperature driven by changes in sea level pressure in the North Pacific (Hare and Mantua 2000). A major climate regime shift occurred in 1977 associated with intensification of the Aleutian low pressure system, stronger cyclonic flow around the Alaska Gyre, warmer ocean temperatures, and changes in the marine ecosystem. In combination, these oceanographic and atmospheric influences introduce both high frequency (e.g., interannual) and low frequency (e.g., intra- and inter-decadal periods) variability into the marine ecosystem.

The glaucothoe molt into a benthic, largely solitary, existence as the first red king crab instars during May to July around Kodiak; preferred habitat is nearshore, rocky substrate with high-profile sessile fauna (Powell and Nickerson 1965; Armstrong et al. 1993; Stevens and Kittaka 1998; Loher 2001). Molt frequency declines from 7 to 8 molts the first year after settlement to 1 to 2 molts in the fourth year (McCaughran and Powell

1977). Early stage instars, and newly molted crab, are highly susceptible to predation by a wide variety of shellfish and groundfish, including cannibalism (Broderson et al. 1990). General increases in the predator biomass in the Gulf of Alaska during the 1970s are well recognized (Hollowed and Wooster 1992; Anderson and Piatt 1999; Hare and Mantua 2000; Ciannelli et al. 2005). However, predation on any king crab life stage has been poorly documented (Albers and Anderson 1985; Livingston 1989; Dew and McConnaughey 2005; Zheng and Kruse 2006), likely due to biases in available diet data related to several factors: (1) historically, few groundfish stomach samples were collected in nearshore, shallow waters inhabited by juvenile crab; (2) sampling of predator stomachs in deeper waters typically occurred in summer, not during late winter to spring when most adult crab undergo ecdysis and are most vulnerable to predation; and (3) extensive sampling of predator stomachs in recent years occurred during low red king crab abundance when alternate prey are more prevalent.

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Appendix B. Management Strategy Evaluation

B.1 Past Patterns and Current Practices

The commercial fishery for red king crab around Kodiak Island has remained closed since 1983 with little indication of stock rebuilding to historic levels of higher abundance (Sagalkin 2008). Although the stock abundance would need to increase considerably before a fishery would be allowed, it may be insightful to examine some historical population indices from the perspective of conditions that would need to be met prior to fishery implementation. This is intended to be more of a cursory examination rather than a comprehensive analysis.

Under a management plan adopted by the Alaska Board of Fisheries in 1995, several criteria must be met before a commercial fishery for red king crab would be allowed to reopen (Pengilly and Schmidt 1995; Sagalkin 2008). First, abundance of female crab must exceed a threshold of 5.12 million fertilized females; this threshold is further allocated across individual management districts around Kodiak Island. Second the harvest rate must not exceed 20% of the mature male abundance. Third, the harvest abundance must not exceed 60% of legal male abundance. Although the current management strategies were not adopted until 1995, population abundance data derived

from Bechtol and Kruse (*in press* a) were used to examine harvest rates during the years 1960 to 1982 from the perspective of the current management strategies.

The minimum size limit for legal retention of male red king crab for most fishing years and management districts in the Kodiak Management Area was 178 mm carapace width, equivalent to ~145 mm CL (Blau 1988). Therefore, legal males for this analysis were defined to be animals ≥ 145 mm carapace length (CL). Due to growth variability of individual crab, some males in this "pre-legal" stage actually have a legal carapace width, and visa-versa. Additionally, some harvests of sublegal males occurred because realistic enforcement of minimum legal size typically allows landings of a small proportion of sublegal crab (personal observation). These crab definitions are therefore used as a generalization for retrospective analyses with the recognition that deviations exist but are generally small and likely had little effect on the results.

In the Kodiak area, male size at physiological maturity (75 to 85 mm CL), the size at which sperm are produced, is smaller than size at functional maturity (≥ 130 mm CL), the size at which males have been observed in mating pairs (McCaughran and Powell 1977). Pre-legal crab, as defined in Bechtol and Kruse (*in press* a) based on the growth increment research of McCaughran and Powell (1977), are believed to be one molt smaller than legal size and include males that are ≥125 mm CL and <145 mm CL. However, a spawner-recruitment analysis indicated that pre-legal crab make a significant contribution to reproductive effort of the Kodiak red king crab population (Bechtol and

Kruse *in press* b). Thus, the abundance of mature males for the purpose of this analysis is defined as the total of legal and pre-legal crab.

To evaluate the historical harvest patterns, the observed annual harvest rate of mature males was defined as the total annual harvest abundance divided by the total mature male abundance. The observed harvest rate of legal males was calculated as total annual harvest divided by the legal male abundance.

Results indicate the current harvest cap of 60% of the legal males would have been exceeded only in the last year of the fishery (Figure B-1). There is also evidence that the harvest rate on legal males was sustained at a relatively high level in the late 1960s, although the threshold was never exceeded during that period. However, the current harvest limit of 20% of the mature males was dramatically exceeded in the late 1960s and the early 1980s with minor overages observed in the early and mid 1970s (Figure B-1).

Stock abundance estimates of female red king crab around Kodiak Island are not available prior to 1972, the year the Alaska Department of Fish and Game implemented fishery independent stock surveys. However, data reported in Bechtol and Kruse (*in press* a) does not include the abundance of fertilized females in the Kodiak population, but estimated abundance of mature females is reported. Mature female abundance undoubtedly exceeds abundance of fertilized females, particularly when the sex ratio was skewed toward in years of high male harvest rates (Bechtol and Kruse *in press* a), but for

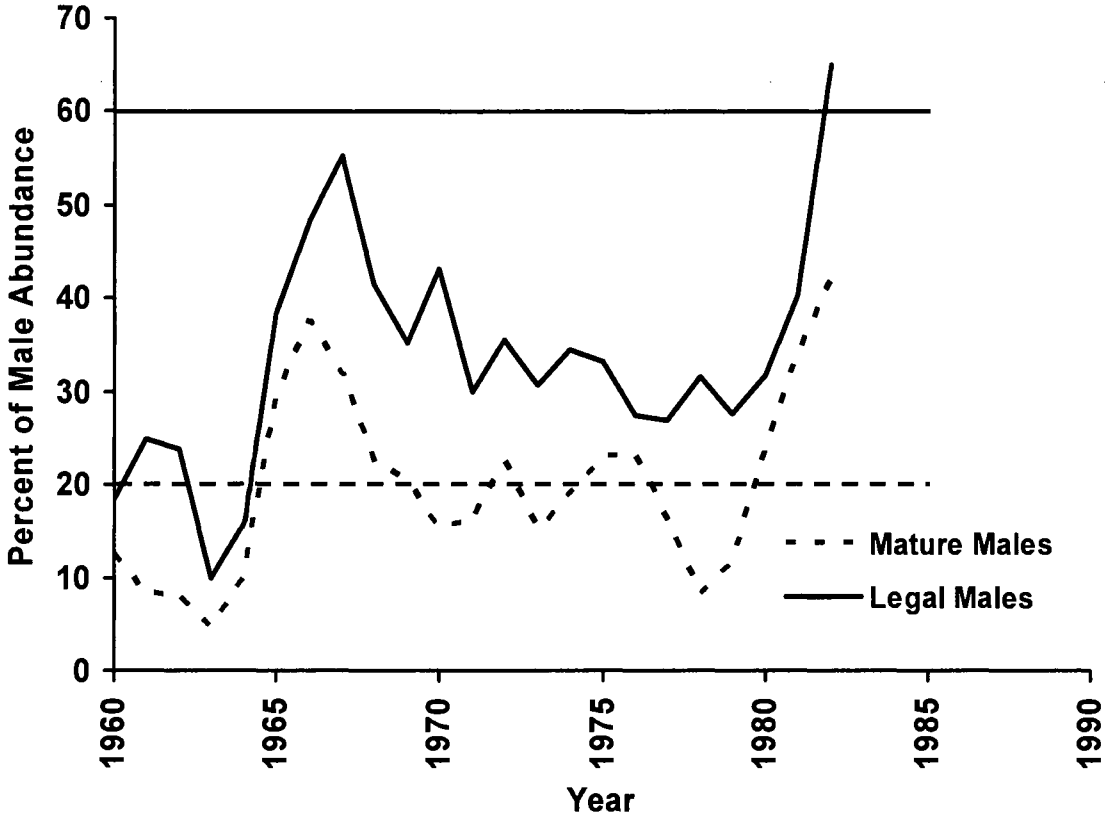

Figure B-1. Observed commercial harvest rates of legal males (solid lines) and mature males (dashed lines) for red king crab at Kodiak, Alaska during 1960–1982. Straight horizontal lines represent management harvest caps adopted in 1995.

this analysis is treated as a proxy for fertilized females. Mature female abundance was above the current threshold of 5.12 million mature females for the Kodiak Management Area from 1972 to 1981 and would not have prevented implementation of a fishery (Figure B-2). It cannot be determined whether mature female abundance would have fallen below the thresholds in localized management districts, but localized depletion is likely as the total population abundance declined and approached the management threshold. In addition, it appears that 1982 was a critical year for the population as estimated mature female abundance fell below the area-wide threshold at the same time that harvest caps were exceeded for both legal males and mature males.

The patterns in male harvest rates with respect to the current harvest regulations adds further support to the hypothesis that excessive fishing pressure was a major contributing factor in the collapses of the Kodiak red king crab stock (Bechtol and Kruse *in press* a). This was particularly true in the early 1980s, a period of increasing harvest rates on a rapidly declining population. The minimum mature female threshold currently in regulation would have curtailed commercial fishing in 1982, and likely sooner as female abundance failed to achieve management thresholds in local districts around Kodiak Island. However, this review is also offered from the perspective of biological information and management strategies that were not available, or not employed, at the time of the stock collapse. For example, fishery managers actively monitored indicators of legal male crab abundance and set harvest guidelines based on legal male abundance (Figure B-1). But current practice for crab management also considers mature male and mature female abundance.

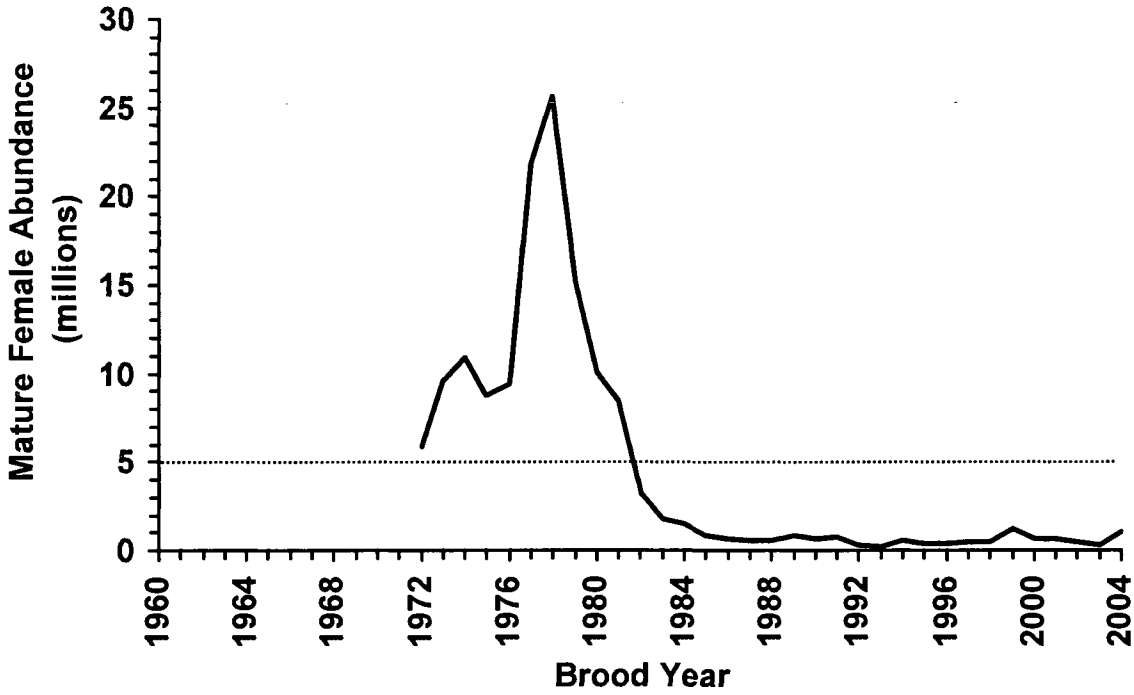

Figure B-2. Estimated mature female abundance for the red king crab population around Kodiak Island during 1972–1981. The dotted horizontal line represents the current management threshold for mature females.

B.2 References

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Appendix C. Spatial Patterns in the Commercial Fishery for Kodiak Red King Crab

C.1 Abstract

Gulf of Alaska waters around Kodiak Island once supported the world's largest fishery for red king crab, *Paralithodes camtschaticus*. Fishery harvests occurred at low levels beginning in the 1930s, but increased rapidly in the 1960s to a peak harvest of 42,800 mt in 1965. However, stock abundance declined dramatically in the late 1960s, and again in the early 1980s. The history of the fishery included a variety of management measures, such as time and area closures and changes to minimum size limits. Despite these efforts, the stock was ultimately recognized as depleted, and a commercial fishery closure since 1983 has not resulted in a stock recovery. We developed a quantitative retrospective analysis to understand the conditions surrounding the rise, collapse, and continued depleted status of the red king crab stock around Kodiak Island, Alaska. A first step in this approach was to analyze spatial and temporal changes in commercial fishery harvests in response to changes in fleet efficiency. During a critical time of fishery development in the late 1960s, a chance period of strong recruitment helped promote the capitalization of this fishery. Very high harvest rates in the late 1960s were not sustainable, likely due to reproductive failure associated with sex ratios skewed toward females following a recruit-driven fishing period in the 1970s. Environmental and ecological changes, associated with a climate regime shift, likely exacerbated these problems.

C.2 Introduction

Waters around Kodiak Island in the northern Gulf of Alaska (Fig. C-1) once supported the world's largest fishery for red king crab, *Paralithodes camtschaticus*. A U.S. domestic fishery developed slowly during the 1930s to 1950s, as operators of purse seine vessels (i.e., < 18 m overall length) sought to supplement their summer salmon harvests by exploring crab fishing in the Kodiak area during winter (Gray et al., 1965; Spalinger, 1992). The lack of live tanks and small vessel size limited the fishery to nearshore areas adjacent to seaports with processing facilities. Annual landings increased rapidly in the 1960s to a record harvest of 42,800 mt (94.4 million lb) in 1965, but harvests were not sustainable and the commercial fishery exhibited a series of declines before being closed in 1983 (Fig. C-2; Spalinger and Jackson, 1994). A variety of management actions, such as time and area closures and changes in minimum size limits, failed to stop the decline of this male-only fishery (Gray et al., 1965; Spalinger, 1992). Moreover, closure of the commercial fishery since 1983 has not resulted in recovery of this severely depleted stock.

As part of a retrospective analysis to better understand the conditions surrounding the rise, collapse, and continued depressed status of the red king crab stock around Kodiak

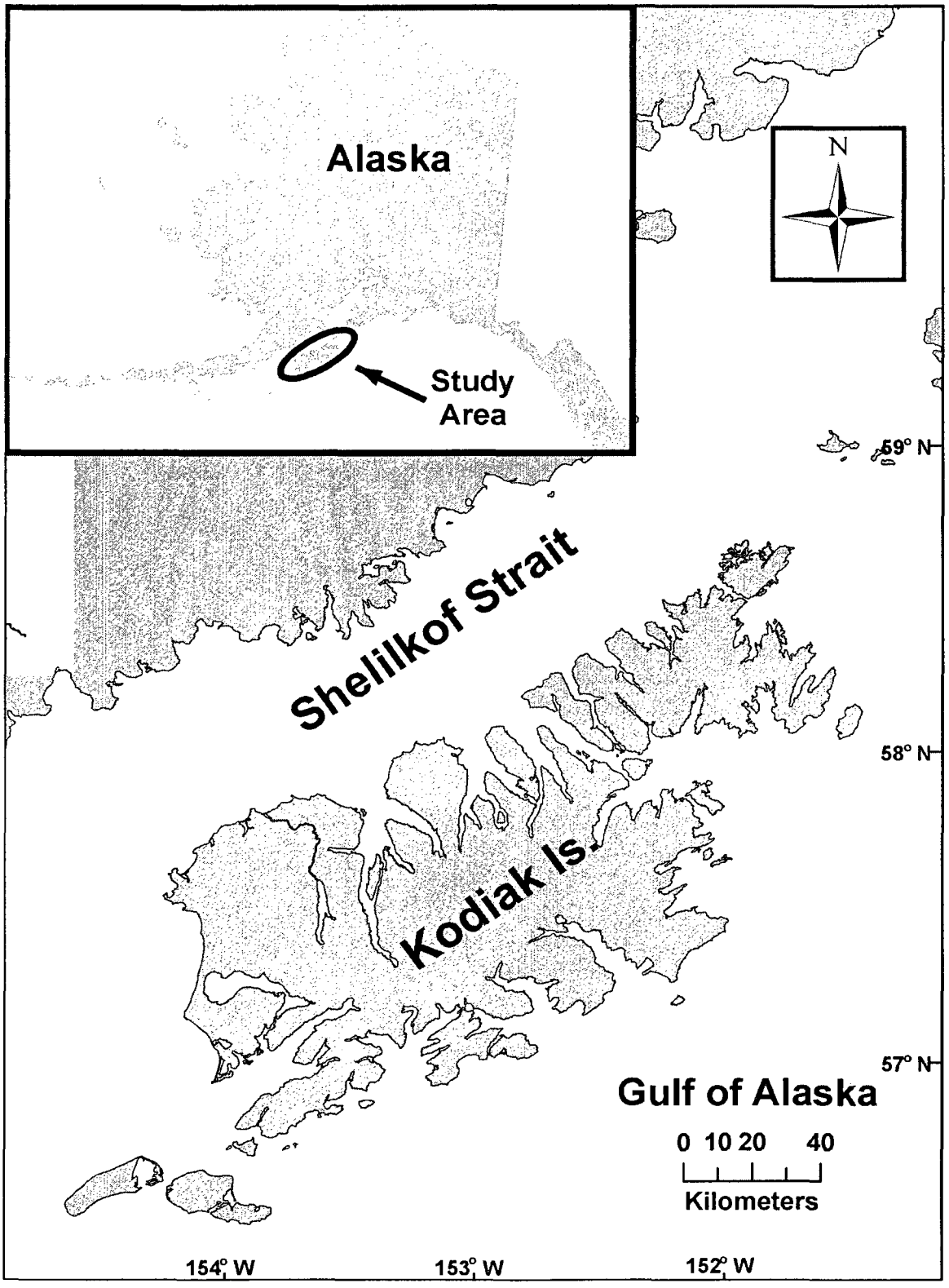


Figure C-1. Location of the Kodiak Island study area in the northern Gulf of Alaska.

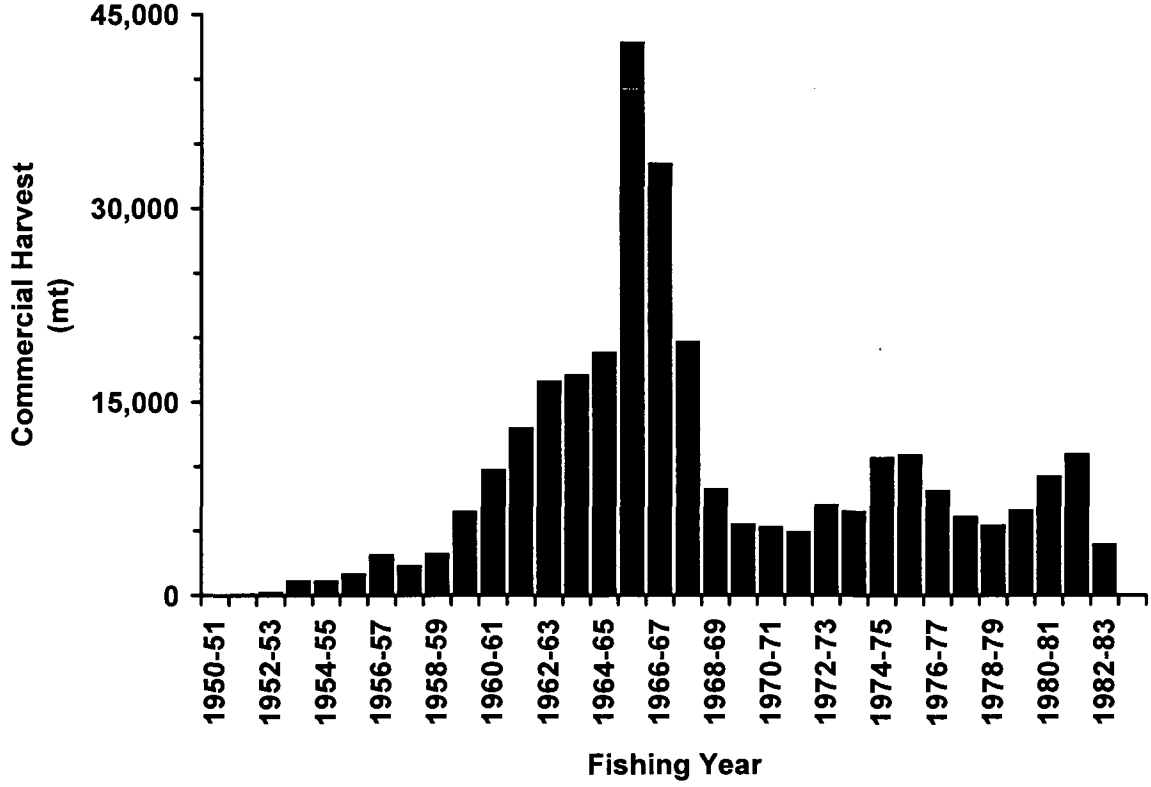


Figure C-2. Commercial harvests of red king crab from the Kodiak Island management area, 1950–1983.

Island, we used a geographical analysis to identify the temporal and spatial changes in the distribution of the crab harvests.

C.3 Methods

Fishery harvest data were compiled from the Alaska Department of Fish and Game (ADF&G) databases and summary reports. Harvest data for 1950-1968 were primarily obtained from published reports (e.g., Gray et al., 1965; Spalinger and Jackson, 1994; Cavin et al., 2005; K. Spalinger, ADF&G, Kodiak, pers. comm.). The spatial resolution of this "early" data was relatively coarse with little information on catch composition. Harvest data for 1969 through 1982 were obtained from the ADF&G TIX database (G. Smith and M. Plotnick, ADF&G, Juneau, pers. comm.). Although the Kodiak commercial fishery has been closed since 1983, limited king crab harvests have occurred under subsistence fishing regulations. Subsistence data are available for 1988 to present from ADF&G staff, but, due to uncertainty about data quality, these data were not incorporated into our analysis. Commercial harvest data were pooled per State of Alaska guidelines to protect the confidentiality of individual landing records.

To understand spatial changes in the fishery over time, harvest data were compiled according to the ADF&G statistical reporting areas from the early 1970s (Powell, 1971). These reporting areas were based on a combination of habitat considerations, particularly

depth and distance from shore, and results from crab mark-recapture studies (G. Powell, Kodiak, Alaska, pers. comm.). With few exceptions, harvests in the ADF&G TIX database could be readily assigned to statistical reporting areas from the early 1970s. For data compiled from ADF&G reports for the 1950-1968 period, harvests recorded from specific management "sections" were assigned to discrete statistical harvest areas based on: (1) geographical descriptions of the primary harvest sites given in ADF&G reports; (2) descriptions of the prevailing harvest patterns at the time of the harvest; and (3) proportional harvest patterns in adjacent years. The statistical harvest area map was obtained as a set of hand-drawn digital polygons (D. Urban, ADF&G, Kodiak, Alaska, pers. comm.). Polygons were edge-matched, and then clipped to an Alaska land polygon. Harvest data were joined to statistical area polygons and graduated symbol maps created from 5-year averages of the harvest data. Georeferenced data (NAD 83) were projected as Universe Transverse Mercator (UTM) in a geographical information system (ArcGIS version 9.1, ESRI, Inc.).

In addition to a visual examination of the spatial distribution of the harvest over time, the spatial analysis includes several descriptors of the catch. Because we were interested in general trends across the longer time frame of the fishery, we used 5-year averages of catch from 1950 to 1982. First, the annual harvest biomass was summed across the Kodiak study area and averaged over each 5-year fishing period, herein referred to as "average annual catch." Second, the total number of statistical harvest areas from which catch was reported over the 5-year period is referred to as the "number of reporting

areas;" this number gives an indication of the spatial breadth of the fishery. Finally, harvest per area, defined as the total harvest divided by the number of reporting areas, indicates the harvest intensity in the fished areas. Note that only those areas where catch occurred were included in the harvest per area, and that only two fishing seasons (1981-1982 and 1982–1983) were included in the harvest per area for the final years of the fishery.

Our original intent was to incorporate a spatial analysis of environmental patterns in conjunction with recruitment and fishery patterns. However, our efforts were compromised by several factors. First, the most dramatic changes in fishing patterns occurred during the late 1950s to late 1960s, a period with poor spatial resolution in the harvest data. For our analysis here, it was necessary to "assign" a substantial portion of the catch to statistical areas based on ADF&G annual report summaries and prevailing fishing patterns at the time of the harvests. However, there remains substantial uncertainty in this spatial allocation of the catch. Second, the pot and trawl surveys were conducted well after the peak fishing years and at a time when crab population abundance was declining or had crashed. The geographic distribution of the pot survey, conducted from 1972 to 1986 around the east, south, and southwest sides of the Kodiak archipelago, was substantially less than the distribution of the harvest. Pot survey spatial resolution was also fairly coarse, with survey stations that were generally replicated on an annual basis. Spatial coverage by the trawl survey, conducted since 1986, has been even more reduced compared to the pot survey. The trawl survey also focuses on Tanner crab habitat

and so has a spatial bias against red king crab. As a result, it is difficult to extrapolate meaningful relationships in population dynamics from the stock level to spatial patterns at the localized level of production. Third, environmental data for the area around Kodiak Island are also limited spatially and temporally. For example, long-term datasets for the northern Gulf of Alaska have primarily been collected at the GAK line off Seward and at Trident Basin in Chiniak Bay, Kodiak. The GAK data represent upstream conditions in the Alaska Coastal Current, whereas the Trident Basin temperature data represent nearshore conditions on the east side of Kodiak Island. However, data was not collected from either location until the 1970s, again, well after the peak fishery years. Although various time series of environmental data have become available as a result of simulation modeling (e.g., sea surface temperature data available through the NOAA National Operational Model Archive and Distribution System), there remains little historical information of subsurface conditions. Thus, these spatial and temporal inconsistencies made it difficult to identify meaningful spatial relationships between survey and fishery catches, environmental patterns, and, ultimately, crab recruitment.

C.4 Results

During the early 1950s, fishing was confined to inshore, shallow areas near ports of landing (Fig. C-3a). Harvests occurred in thirteen reporting areas, representing only eight bay or cape areas. With average annual catch of 549 mt, 39% (214 mt) which came from

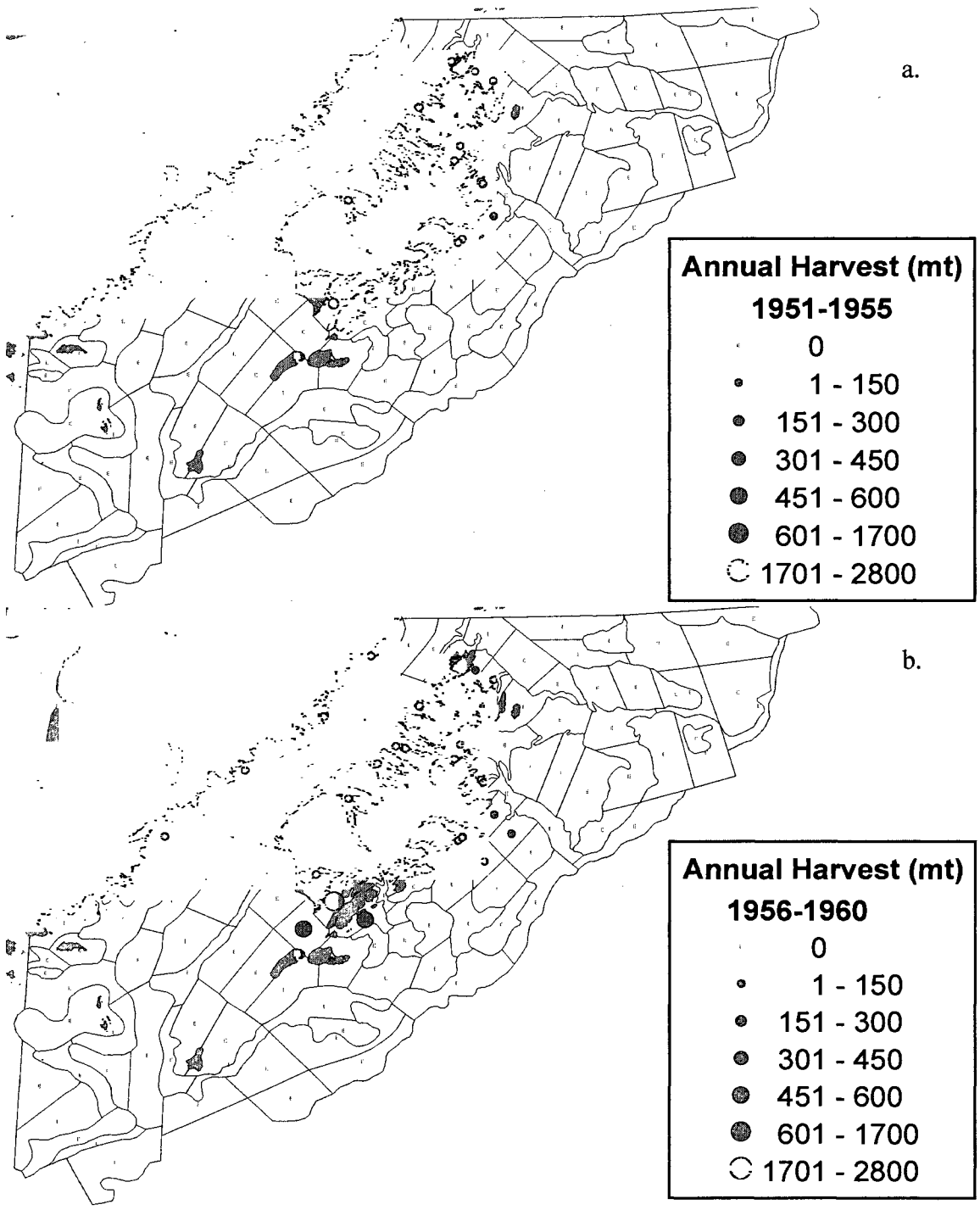


Figure C-3. Distribution of commercial harvests of red king crab around Kodiak Island. Polygons designate statistical reporting areas.

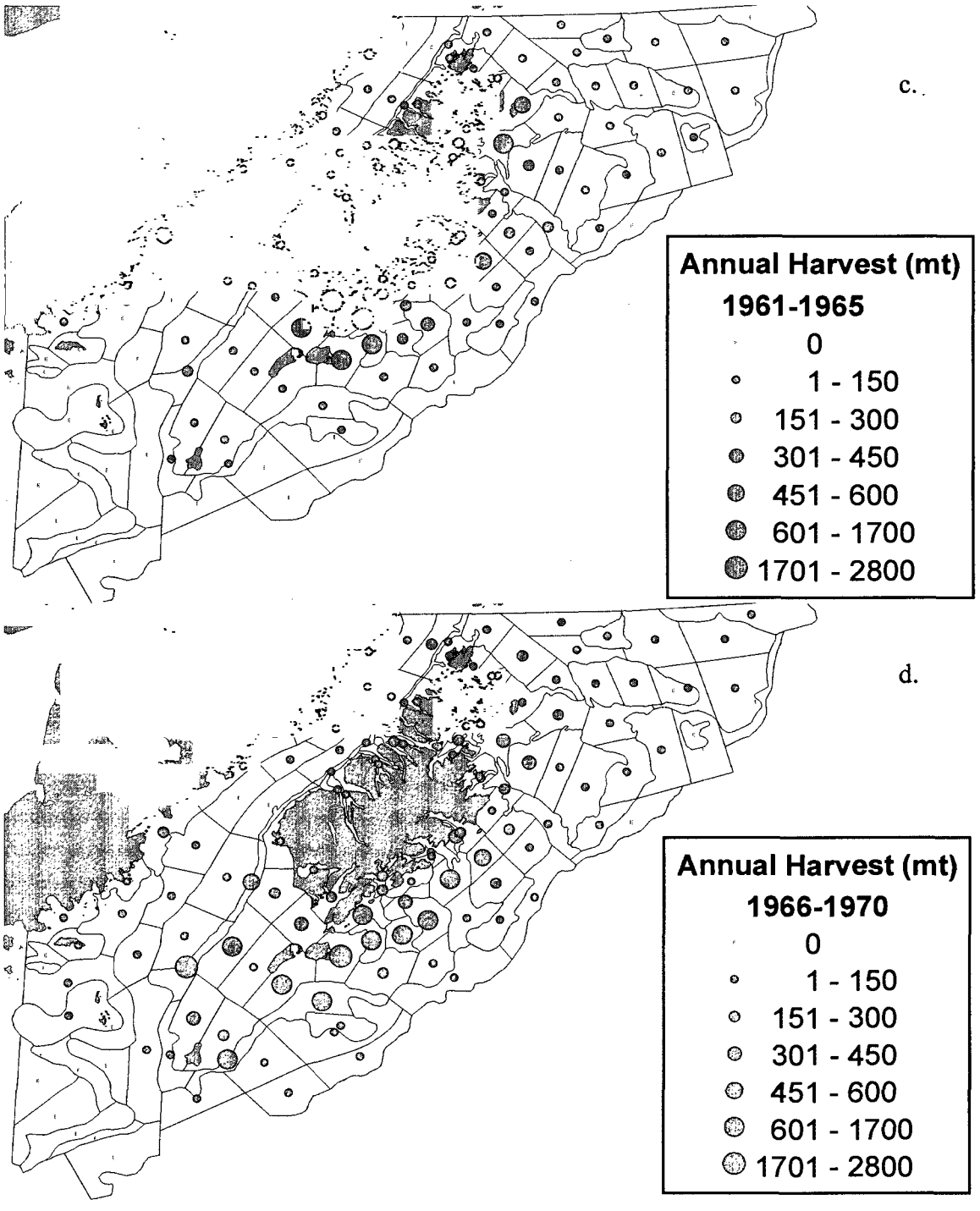
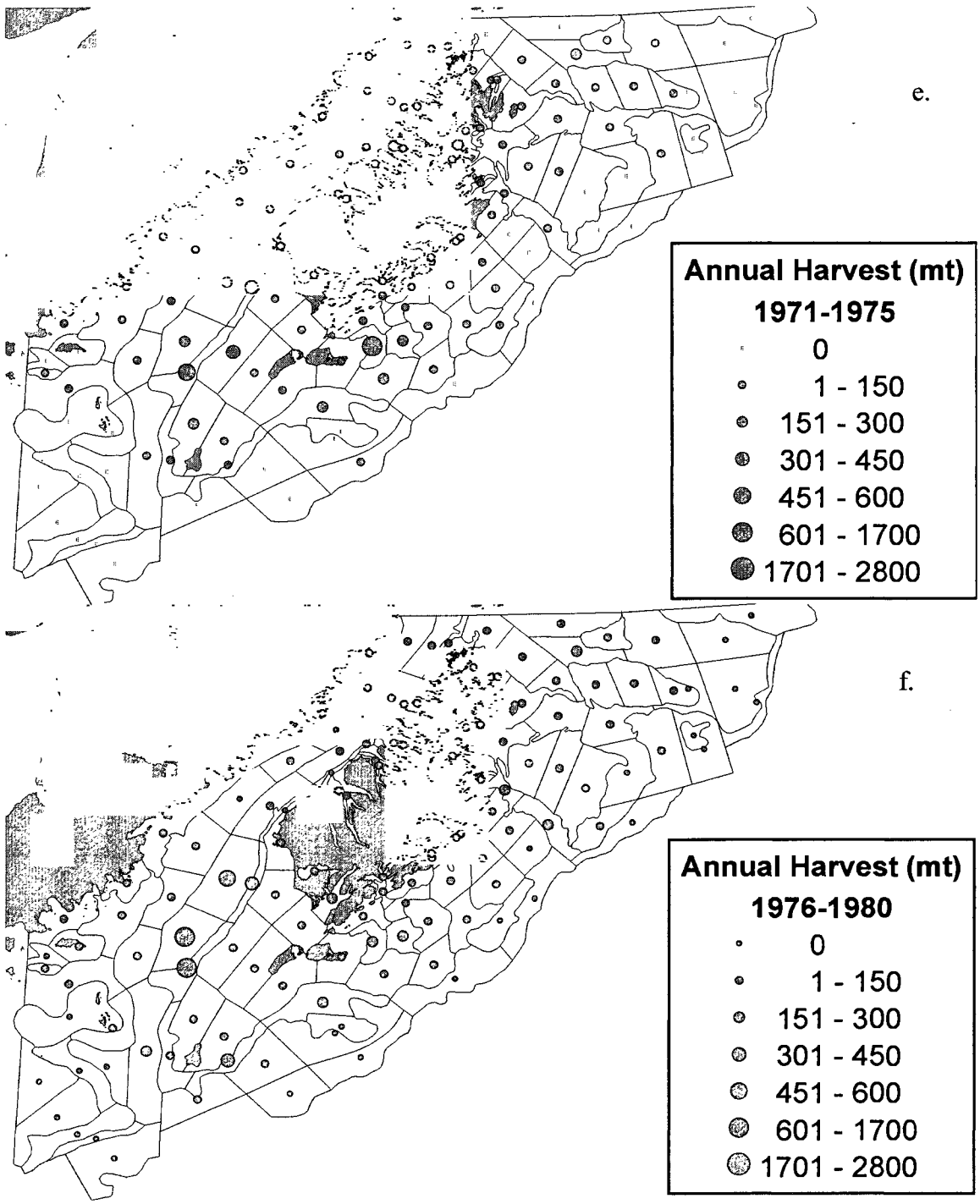


Figure C-3. (continued)



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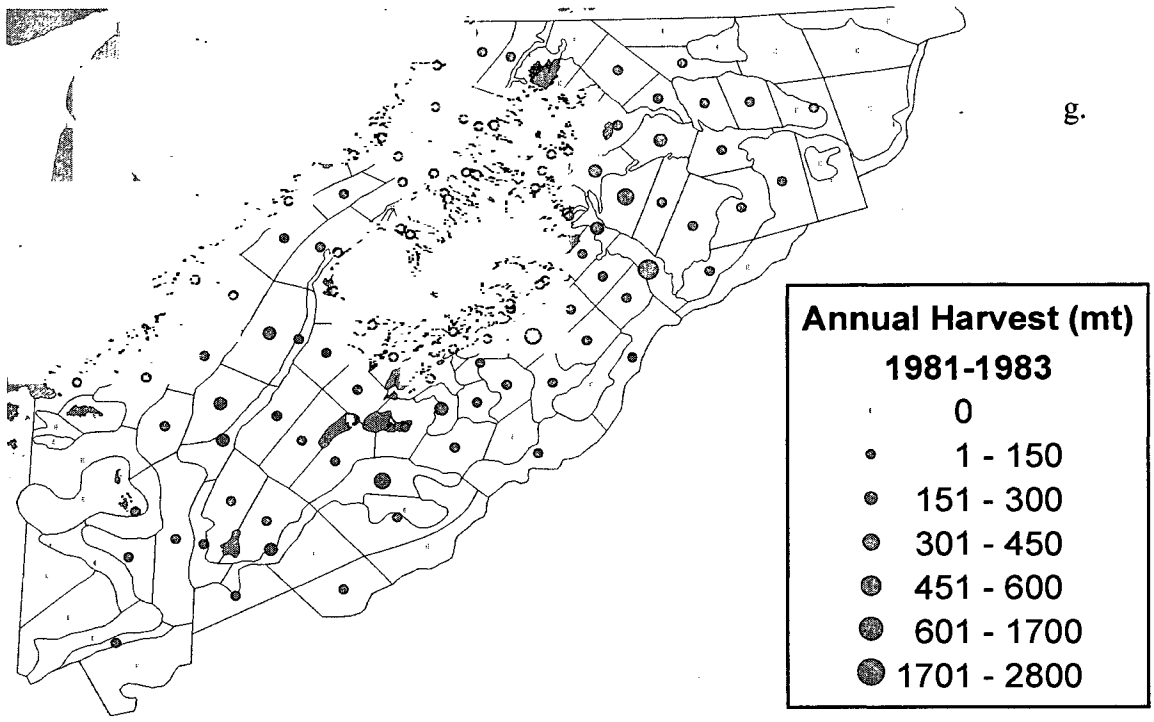

Figure C-3. (continued)

Alitak Bay on the southwest end of Kodiak Island, the harvest per area was 42 mt. In addition to providing access to landing facilities, approximately half of the harvest areas were bays with deep fjords that offered protection from inclement weather.

During 1956-1960, the number of reporting areas from which crab were harvested nearly doubled to 24 (Fig. C-3b). Although catch remained low in most areas, including some exploratory fishing areas on the north side of Shelikof Strait, average annual catch was nearly 3,400 mt with 78% (2,626 mt) again coming from the southwest side of Kodiak Island, including over 2,100 mt from inside and immediately adjacent to Alitak Bay. Harvest per area increased threefold over the early 1950s to 141 mt.

During 1961-1965, crab were harvested from 99 reporting areas, as the advent of larger vessels equipped with flowing seawater live tanks and dedicated full-time to crab fishing allowed exploration of fishing grounds farther from port. Although the harvest per area of 153 mt was a relatively small increase from the late 1950s, the average annual catch across the management area increased substantially, to over 15,000 mt, as a result of the expanded spatial distribution of the fishery. Waters southwest of Kodiak Island remained strong producers, but substantial harvests also occurred along the southeast and eastern sides of the Kodiak Archipelago and also in Shelikof Strait north, and particularly west, of Kodiak (Fig. C-3c).

Annual landings peaked at 43,400 mt (95 million lb) in the 1965-1966 season, but by the late 1960s, inshore areas were becoming depleted and annual catches fell to about 5,500 mt by 1969 (Fig. C-2). However, during 1966-1970 harvest occurred in 115 reporting areas (Fig. C-3d), virtually throughout the management area as vessel efficiency (and mean vessel size) continued to increase. Average annual catch was 21,400 mt during this 5-year period, and harvest per area was 186 mt. Areas of greatest harvest were located along the southern to southwest sides of Kodiak and a decrease in catches from Alitak Bay and northeast Kodiak was evident.

During the early 1970s, average annual catch across the management area fell to 5,600 mt annually. Harvests during this period occurred in 96 reporting areas, and harvest per area was 69 mt. Thus, the geographic distribution of the harvest only decreased by about 17% but the average yield per producing area decreased 63% (Fig. C-3e), suggesting intensive searching by the fleet to maintain catches. Reporting areas producing the largest catches were limited to the southwest end of Kodiak.

Slight increases in annual harvests to just under 11,000 mt during the 1974-1975 and 1975-1976 seasons and also the early 1980s were likely driven by strong recruitment (Fig. C-2). Average annual catch during 1976-1980 was 7,000 mt from 103 reporting areas, averaging 68 mt per area producing catch. The areas producing the largest catches during this period was the trench in southern Shelikof Strait, with relatively low catches distributed throughout the management area (Fig. C-3f).

During the early 1980s, average annual catch fell to 5,100 mt. The fishery continued to be widely disbursed spatially with harvest reported from 100 areas, but the harvest per area of 51 mt, the lowest level since the fishery exploratory phase of the early 1950s, again suggests extensive effort by the fleet to obtain catches (Fig. C-3g) The areas producing the largest catches were limited to offshore areas south and east of Kodiak Island. Based on dramatic and rapid declines in fishery-independent data during the early 1980s, the commercial fishery was closed in 1983 and has remained closed due to a lack of evidence of significant recruitment.

A geographic expansion of the red king crab fishery took place during the 1960s and 1970s. This expansion was associated with an increase in fishing capacity associated with increased vessel participation by full-time crab fishing vessels with flowing seawater live tanks capable of staying at sea for prolonged periods of time. As a coincidence, the expansion of the late 1960s occurred during with a period of strong crab recruitment that sustained a growing fishery for a short period of time. Once recruitment declined in the late 1960s, exploitation rates escalated, sex ratios became skewed toward mature females, and reproduction appears to have been compromised. In the 1970s, a few moderately strong year classes sustained the now recruit-driven fishery until the early 1980s, when the population was beset by recruitment failures. Pot survey data reveals a dramatic decline in the spatial distribution of the population from the early 1970s to the mid 1980s (Fig. C-4; Johnson 1990). Despite fishery closure since 1983, the stock has failed to

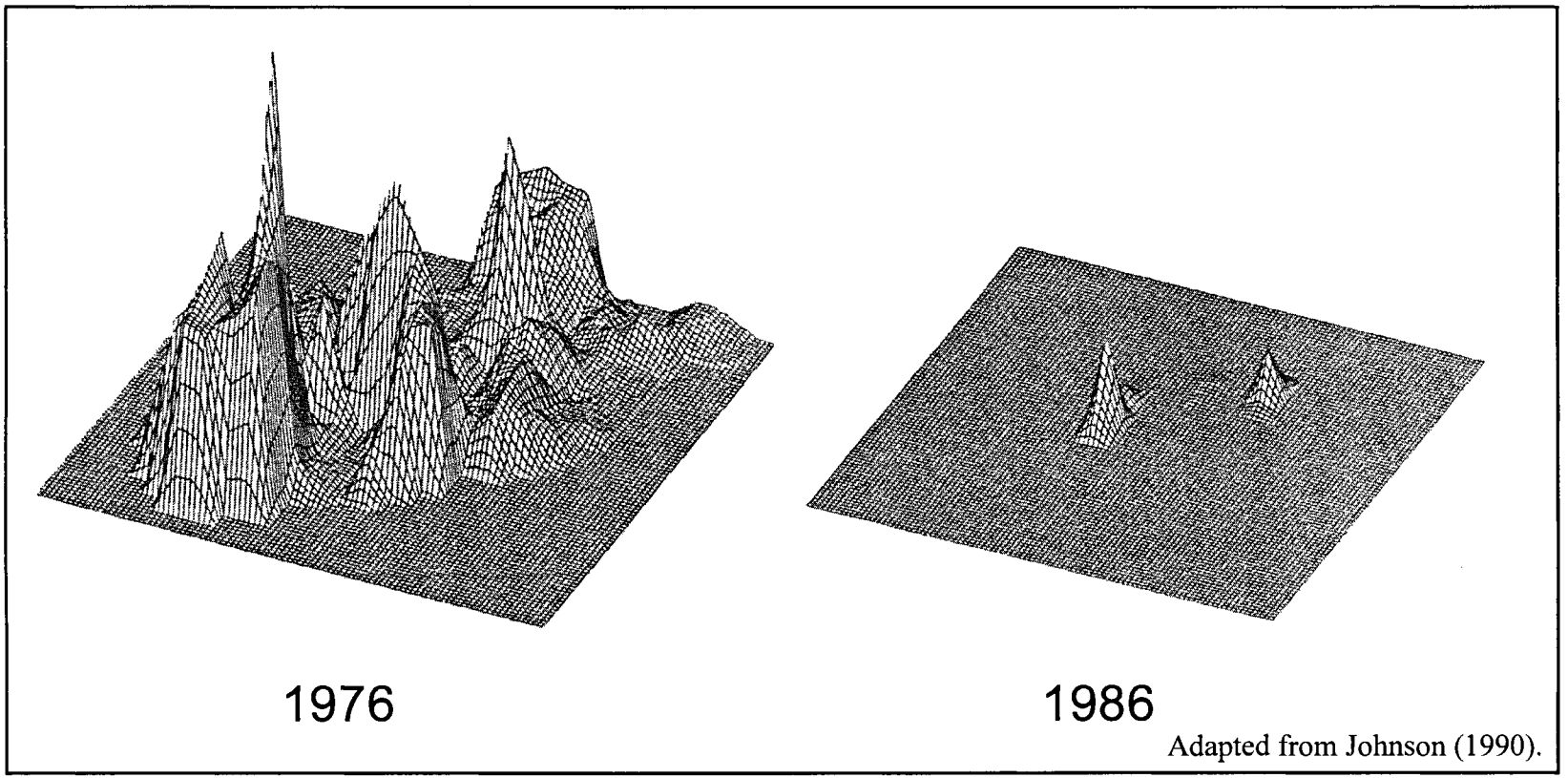

Figure C-4. Declines in abundance and geographic distribution of legal male red king crab off Kodiak as evidenced by pot survey catch per unit effort, 1976 and 1986. The x-axis is 157.7-149.5 W long.) and y-axis is 54.5-59.0 N lat.

recover. A climate regime shift in the late 1970s was associated with other ecosystem changes, including an increase in ocean temperatures and increases in the abundance of predatory fishes, such as Pacific cod and Pacific halibut. Among all ADF&G statistical reporting areas, no clear trends are evident in the 5-year averages in pot survey CPUE of Pacific cod or Pacific halibut (Figures C-5 and C-6). However, greater scrutiny of the nearshore areas, those areas most important to early juvenile red king crab, shows a dramatic increase in cod catch over time (Figure C-5). It is postulated that this correlates with increased, but undocumented, mortality on juvenile crab. Halibut CPUE increased dramatically over time in virtually all areas around the Kodiak archipelago (Figure C-5). Both Pacific cod and Pacific halibut are potential predators of red king crab, particularly those crab in either juvenile life stages or any newly molted crab in a soft shell condition. However, there is a paucity of predation data in any king crab life stage or shell condition (Albers and Anderson 1985; Livingston 1989; Dew and McConnaughey 2005; Zheng and Kruse 2006). Subsequent trawl survey data, although biased, indicates a substantial reduction in the distribution of the red king crab population (Figure C-7). Thus, the effect of predation as a constraint to the recovery of the red king crab population to higher abundance levels is speculative based on best available information. Nonetheless, the combination of low reproductive potential and unfavorable environmental conditions has likely contributed to the longstanding depressed status of this stock.

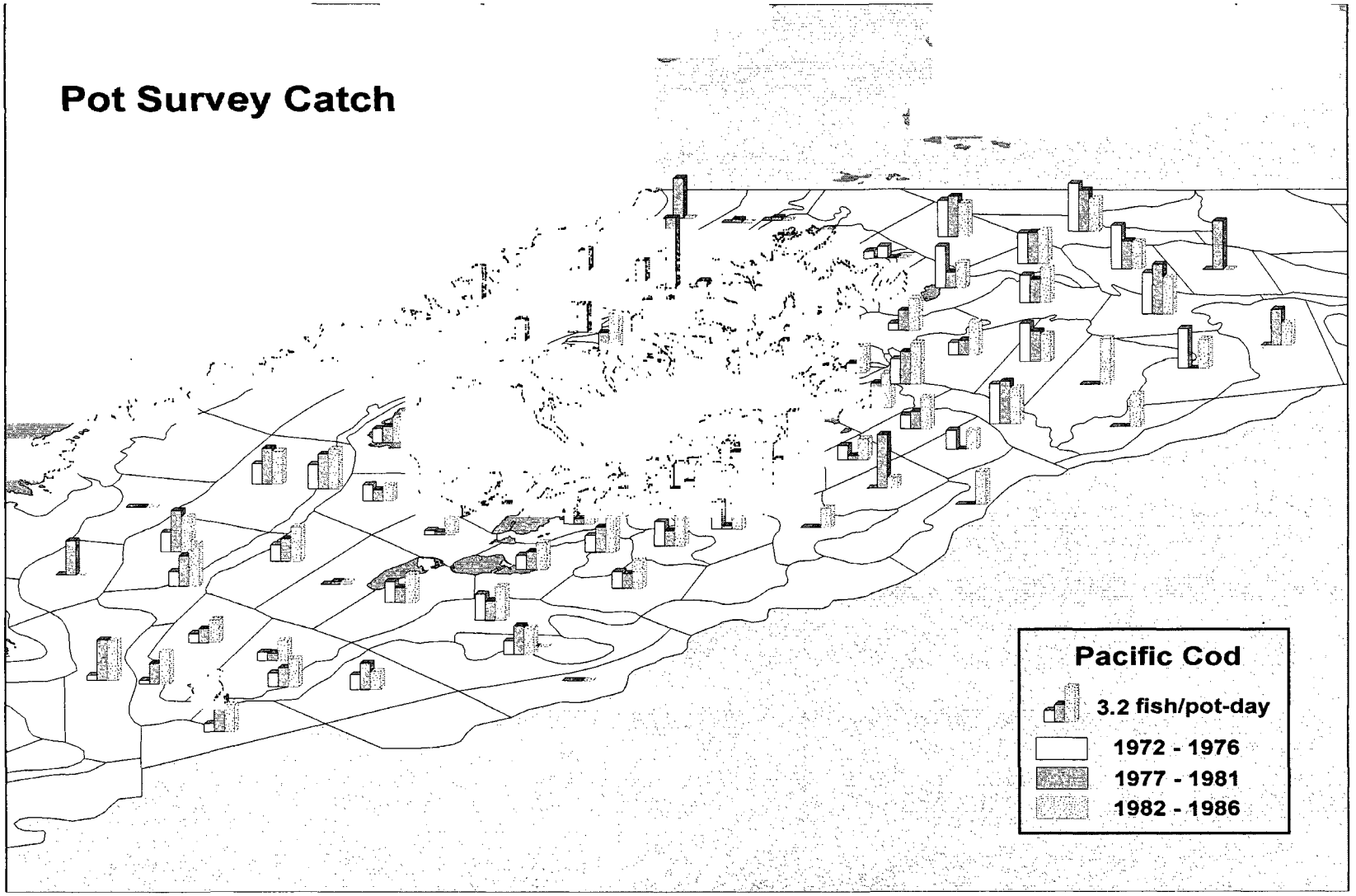

Figure C-5. Catch distribution of Pacific cod in the ADF&G pot survey, 1972–1986.

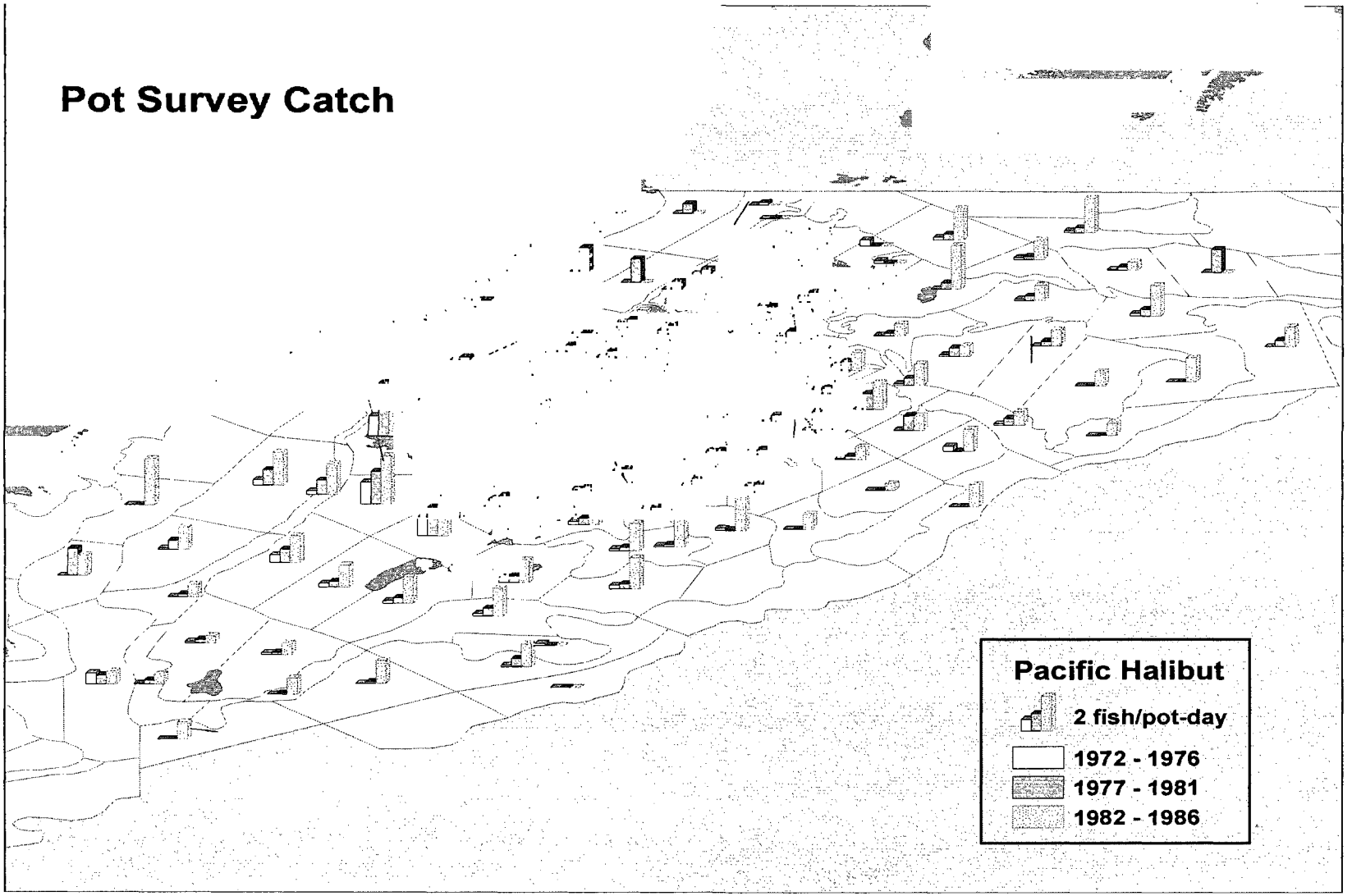

Figure C-6. Catch distribution of halibut in the ADF&G pot survey, 1972–1986.

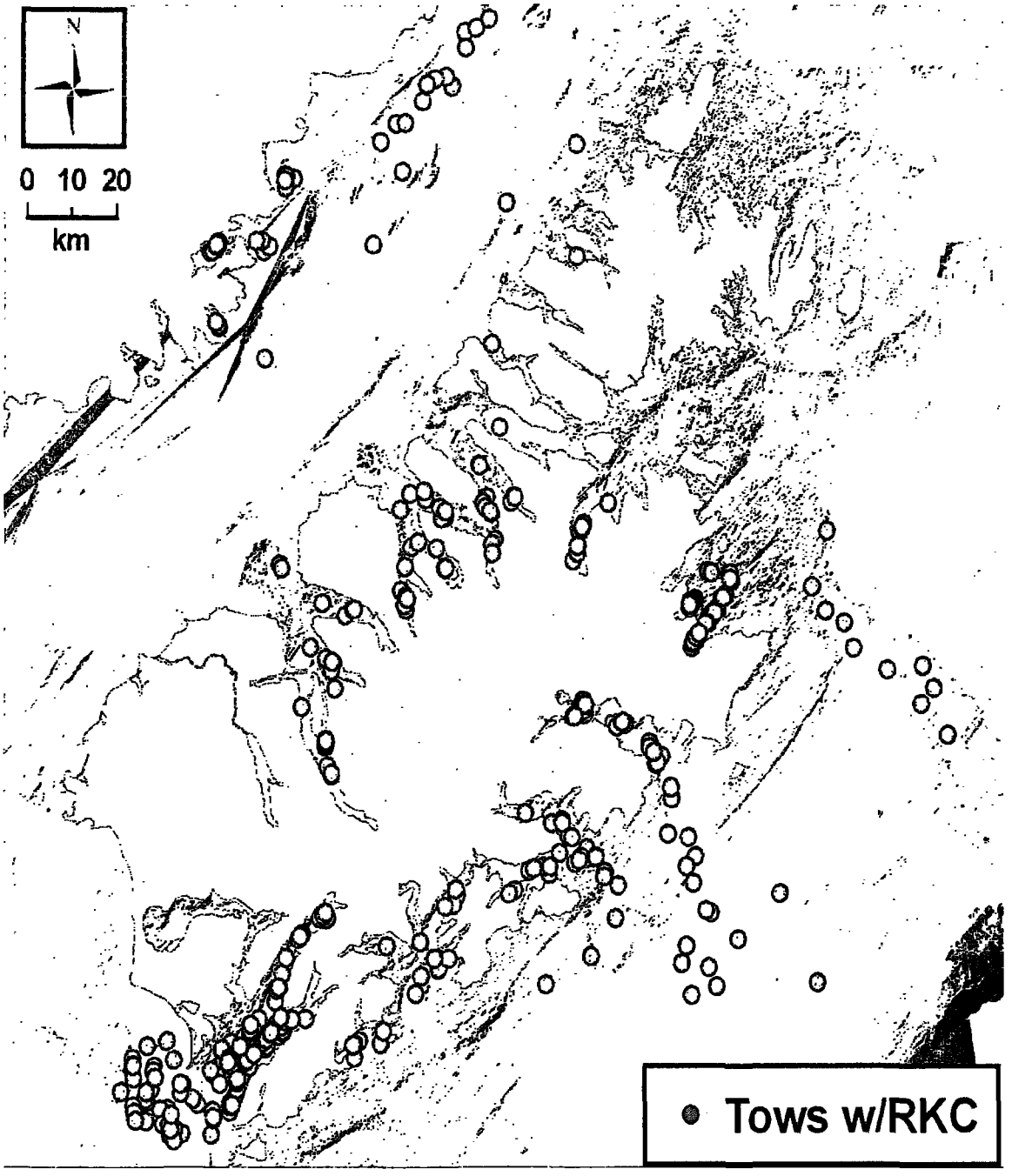

Figure C-7. Bathymetric distribution of ADF&G trawl survey tows with a catch of at least one red king crab, 1980–2004.

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